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INFLUENCE OF WEEDS ON COTTON IN THE SUDAN GEZIRA

FRANK CROWTHER

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RECENT discussions of soil erosion and the results of trials of the various methods of combating it have led agriculturists to re-examine the function of weeds in crop-production. The dictionary states that a 'weed' is a 'wild herb springing where it is not wanted', but there are many 'wild herbs' playing an altogether desirable role in soil conservation that, for want of a better word, are termed 'weeds'. The present paper describes an examination of weed-growth in the Sudan Gezira, designed to find out whether its effect on the cotton crop is wholly deleterious in competing for supplies of nutrients and water, or whether conditions exist where the encouragement of weeds would prove beneficial.

Jacks and Whyte [1] describe a 'selective' system of weeding wherein either weeds are allowed to grow unchecked or weed-stand is adjusted to maintain soil structure for perennial crops like rubber and tea. Cotton, they point out, has earned for itself a bad reputation as a promoter of soil erosion because it requires 'clean weeding'. Therefore the successful cotton-grower has to strike a nice balance between those practices which are immediately essential for crop-production and those which, over a longer period, tend towards soil conservation.

In the rain-grown cotton areas of Africa the liability of erosion to occur during the growth of the crop is frequently offset by the allotment of rest-periods between successive spells of cropping, during which the land produces a natural cover of weeds. Such weeds are distinctly beneficial; they improve the texture, regenerate the fertility of the soil, and at the same time protect it against erosion. So great is such benefit that, in the 'long-grass' area of Uganda it is even found advantageous to *plant* elephant grass (*Pennisetum purpureum*) at the end of the cotton phase, rather than to wait for cover to grow naturally [2]. Again, in the principal rain-area of the Sudan, weeds are allowed to persist almost till the time of cotton-sowing, so that their customary firing will destroy the new with the old and facilitate the subsequent 'clean weeding' of the crop.

All this is in striking contrast to the procedure adopted on cotton areas irrigated artificially. Usually these are cropped intensively with a fixed rotation including cereal and legume. In Egypt, for example, the land rarely remains uncropped for more than three or four successive months, and, as there is practically no rain, weed-growth on such land is negligible. But the Sudan Gezira differs from most irrigated lands in that cotton is grown only twice in a period of 8 years on any particular area, and for 4 or 5 years of the 8 this land is uncropped. The

soundness of long periods of bor[1] has been amply demonstrated by experiment [3]. The average annual rainfall at the Gezira Research Farm, near the centre of the Scheme, is 16 in., and therefore, during bor-periods there is opportunity for weed-development and 'natural regeneration of fertility', akin to that on rain-grown areas.

Regarding resting periods, then, Gezira cotton-lands would seem to hold a place intermediate between the areas of rain-grown cotton and the intensively cropped lands of most irrigation schemes. The present paper describes two experiments which, considered together, test the wisdom of the present practice of 'clean weeding' the land while it is actually under crop and at other times allowing weeds to develop unrestrainedly.

Most of the rain in the Gezira falls from July to September, July and August being the wettest months. In the prevailing high temperatures weeds grow rapidly, ripening off in September and October. On bor-land some of the weeds are grazed off by animals, but the bulk ripens without interference. Meanwhile on the cotton areas the young crop, sown in mid-August, has to compete with the weeds, unless they are rigorously hoed.

A. *'Clean Weeding' of the Cotton Crop*

Normally by sowing-time at least half the year's rain has fallen and weeds, if unchecked, are already abundant. The experiment included, therefore, three treatments up to sowing-time[2] and for each of these comparisons three treatments after sowing, as follows:

Before sowing	*After sowing*
A. Hoed after successive storms, i.e. weeds cut and soil disturbed.	1. Weeds hoed repeatedly from 1 week after cotton germination.
B. Weeds cut regularly without disturbing soil.	2. Weeds hoed from 6 weeks after cotton germination.
C. Weeds left; soil not disturbed.	3. Weeds hoed from 8 weeks after cotton germination.

All hoeing was done by *malod*, a native tool resembling a Dutch hoe. This not only cuts the weeds at ground-level leaving the roots, but also breaks the soil crust. The 'before-sowing' treatments separated these

[1] For convenience the Arabic word *bor* is introduced to signify agricultural land which remains uncropped and uncultivated for at least one whole year. The word 'fallow' hitherto used in accounts of the Gezira Scheme may be ambiguous to readers accustomed to widely different systems of agriculture. Under temperate climates the word implies 'bare fallow' and the opportunity of using drastic and repeated cultivations to destroy noxious weeds. In the same way crops requiring frequent cultivations are sometimes termed 'fallow crops'. By contrast in the tropics 'fallow' denotes undisturbed land with a natural cover of vegetation. Often steps are taken towards the end of the cropping cycle to ensure the rapid establishment of a weed-cover, which may be retained for many years, as in the 'bush fallow' of systems of shifting cultivation. The climatic and agricultural conditions for cotton-growing in the Sudan Gezira differ so completely from these two extremes that the resting periods merit a special name.

[2] Owing to the lightness of July rains in 1940 weed-growth before sowing-time was retarded, and, to obtain an adequate comparison, it was thought desirable to continue the pre-sowing treatments till the end of August.

two effects. Hoeing after successive storms proved more frequent than was necessary to remove the weeds. In treatment B the weeds were cut individually, so that treatments A and B compared the effects of soil-disturbance alone, and B and C, the effects of weed-removal alone. After sowing soil-disturbance is incidental, since the land is irrigated and the rain lessening. Thus treatments 1 to 3 compared varying intensities of weed-competition, from complete freedom from weeds to a state where the crop was visibly stunted before weed-removal. In the entire experiment roots were left in the ground and nothing was removed from the field.

Details of the experiment and the dates of operations were as follows:

	Treatments	*Dates of hoeing*
Sowing: Aug. 16, 1940	A	May 8, 27. June 2, 5
Variety: X1730A (*G. barbadense*)		July 6, 19. Aug. 3, 12, 29
Spacing: 80 cm. between ridges	B	July 17, 28. Aug. 11, 29
Spacing: 40 cm. between holes	C	None
Spacing: 2 plants per hole		
Thinning: To 4 plants. Sept. 15	1	Aug. 29. Sept. 30
Thinning: To 2 plants. Sept. 28	2	Sept. 30
Pickings: Fortnightly from Dec. 26, 1940 to April 3, 1941	3	Oct. 16

9 treatments × 6 replicates = 54 plots. Layout 6 randomized blocks. Gross area 2½ feddans.[1] Net area of one plot = 125 sq. m.

The rainfall in 1940 was 12 in. or 25 per cent. below normal. Where the weeds were left undisturbed they germinated in late July, later than usual; although numerous, they were less potentially menacing than in most years. Subsequent weed-growth under irrigation was normal. The dominant species of weeds were *Phyllanthus niruri* and *Ocimum basilicum*, but *Ipomoea kordofana*, *Hibiscus esculentus* and *Sorghum* spp. were also present. When the weeds were fully developed, there was a carpet about 9 in. thick covering the entire plot.

The cotton crop throughout development was little affected by pest or disease, and, where the weeds were repeatedly hoed, grew vigorously. Where weeding was delayed, especially in treatment C 3, the cotton was severely stunted and yellow during October. Later, after the removal of weeds, leaf-colour became normal but the stunting persisted.

This check to growth is reflected in weight of cotton-leaf dry-matter (Fig. 1). The pre-sowing treatments (Fig. 1 *a*) differed only slightly, but weights were lowest where weeds were not hoed. Delayed hoeing after sowing (Fig. 1 *b*) led to a marked reduction in dry weights. Thus at two months after sowing, where weeds had not been hoed, the cotton-leaf dry-weight was only 47 per cent. of that on the clean-weeded plots of treatment 1, whilst with the 'normal practice' of treatment 2, the corresponding value was 87 per cent. The eventual hoeing of the

[1] 1 feddan = 1·038 acres; 1 kantar seed-cotton = 312 lb.; 1 kantar per feddan = 300·6 lb. per acre; 1 rotl = 0·99 lb.

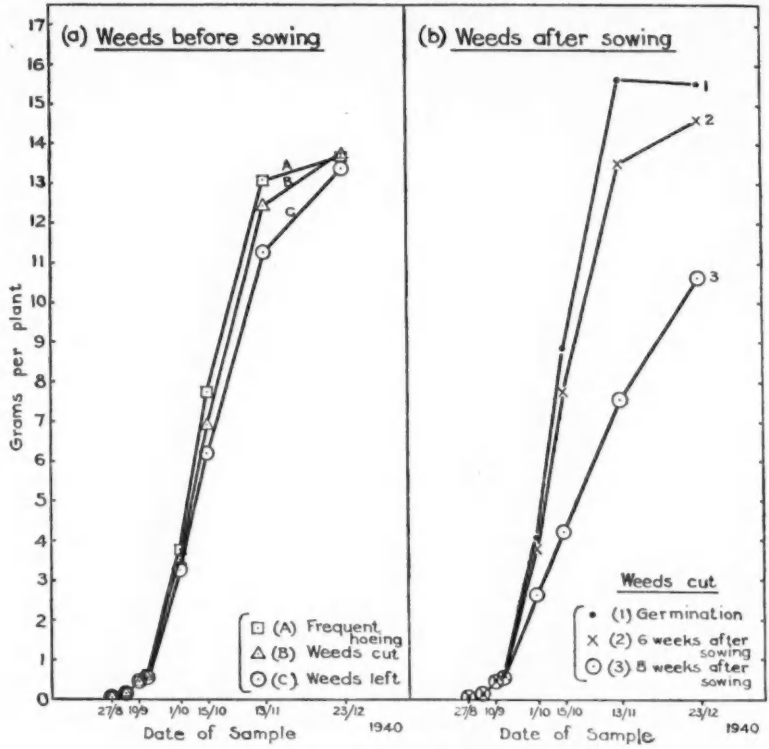

FIG. 1. Effect of weeds on cotton-leaf dry-weight.

weeds in the delayed plots led to additional leaf-production late in the season.

Weed-competition caused leaf-yellowing of the cotton through interference with nitrogen supply, and the extent of this interference is shown in the following mean values for cotton-leaf nitrogen, over the period of 2 to 6 weeks after sowing (September), expressed as percentage of leaf dry-weight:

'Before sowing' weed-treatments		*'After sowing' weed-treatments*	
A. (Hoed)	4·60	1. (No weeds)	4·68
B. (Weeds cut)	4·50	2. (Normal)	4·61
C. (Weeds left)	4·49	3. (Weeding delayed)	4·39

From the regression equation of yield on September nitrogen percentage already published [4] differences of 0·11 per cent. for 'before sowing' and 0·29 per cent. for 'after sowing' treatments indicate yield-differences of 0·8 and 2·3 kantars per feddan respectively. In the present experiment the correlation was modified by the additional nitrogen locked up in the weeds and later made available through the

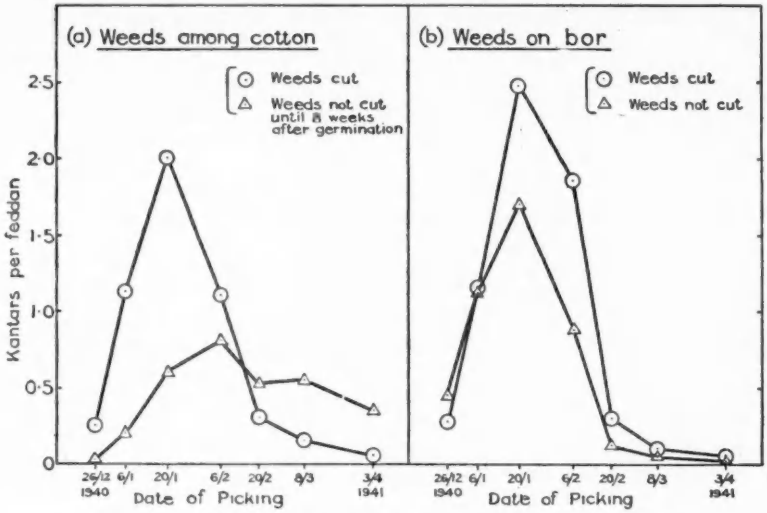

FIG. 2. Effect of weeding of cotton and bor on rates of picking.

last hoeings, which lessened the treatment differences in final yields. These, expressed as kantars seed-cotton per feddan, were:

Treatment Means

Before sowing		*After sowing*	
A. (Hoed)	4·72	1. (No weeds)	5·08
B. (Weeds cut)	4·50	2. (Normal)	4·76
C. (Weeds left)	4·32	3. (Weeding delayed)	3·61
S.E.[1]	±0·130*	S.E.[1]	±0·130**

Separate Treatments

	After sowing		
Before sowing	1	2	3
A	5·14	4·95	4·06
B	5·12	4·65	3·74
C	4·97	4·70	3·03

Figure 2 *a* gives the yields of separate pickings for treatments C 1 and C 3.

The treatment differences observed during the growth of the crop were reflected in the yield-results. Delayed hoeing of weeds, both before and after sowing, depressed cotton yields, and the soundness of the 'clean weeding' practice in the Gezira is thus confirmed. But hoeing was not equally important at all times. Weeds were not very harmful

[1] The asterisks above standard errors in this and subsequent tables refer to significance by the *z* test. Those with one are significant at the 5 per cent. level, with two at the 1 per cent. level, and with three at the 0·1 per cent. level.

before sowing, provided that the weeds growing after sowing were rigorously controlled (treatments A 1, B 1, C 1). When hoeing after sowing was postponed, the yields fell, and the amount of the reduction increased sharply with length of the delay. A delay of 5 weeks reduced the yield by 0·32 kantars per feddan, whilst a further postponement of only another 2 weeks brought the reduction to 1·47 kantars per feddan.

The severity of the competition between crop and weeds depended on the treatment the land received *before* sowing. It was greatest where the weeds were allowed to grow without interference (treatment C). There was less competition where the weeds were removed without disturbing the soil (treatment B), and least of all where the soil was disturbed frequently, by hoeing after storms (treatment A). The reductions in yield with delayed hoeing after sowing were 1·94, 1·38, and 1·08 kantars per feddan for treatments C, B, and A respectively. Frequent hoeing (treatment A) lowered the cotton-ridges so that they were wetted more rapidly. This hastened weed-germination, and the greater the proportion of weeds germinated before sowing, the less serious was the subsequent competition with the young cotton crop, and so the less urgent was the need for later weed-control.

B. *Weeding of Land resting before Cotton*

Since in the Gezira the land is irrigated only when it is cropped or about to be cropped, weed-growth on the bor is entirely dependent upon rainfall. The weeds generally germinate during July, grow rapidly and flower during August and early September. There is some variation among the species, but usually the weeds dry off by late September.

An experiment was laid down in which the normal practice of leaving weeds to grow and ripen freely was compared with regular cutting of the weeds at ground-level, with the *malod*, from late August 1939, when the weeds were growing rapidly, till the end of the rains. The entire area was sown with cotton a full year later, in August 1940. Details of the experiment and dates of hoeing are as follows:

Bor	*Cotton*
Dates of hoeing: Aug. 22, Sept. 2, Oct. 10 and 22, 1939	Date of sowing: Aug. 16, 1940
Layout: 2 treatments, 10 replicates = 20 plots arranged in 10 randomized blocks	Variety: X1730A
	Spacing: 80 cm. between ridges, 40 cm. between holes, 2 plants per hole
	Thinning: to 4 plants, Sept. 15; to 2 plants, Sept. 28
Gross area of experiment: 1¼ feddans	Pickings: fortnightly from Dec. 26, 1940 to April 3, 1941
Area of one plot: 202 sq. metres	

The last differential hoeing was in October 1939 and subsequently the whole area was ploughed for cotton and treated uniformly. The plots of both treatments were kept free from weeds during the 1940 rains.

Rainfall in 1939 was abnormally heavy, 22 in. instead of the normal 16 in. Weed-growth was therefore unusually extensive. At the time of

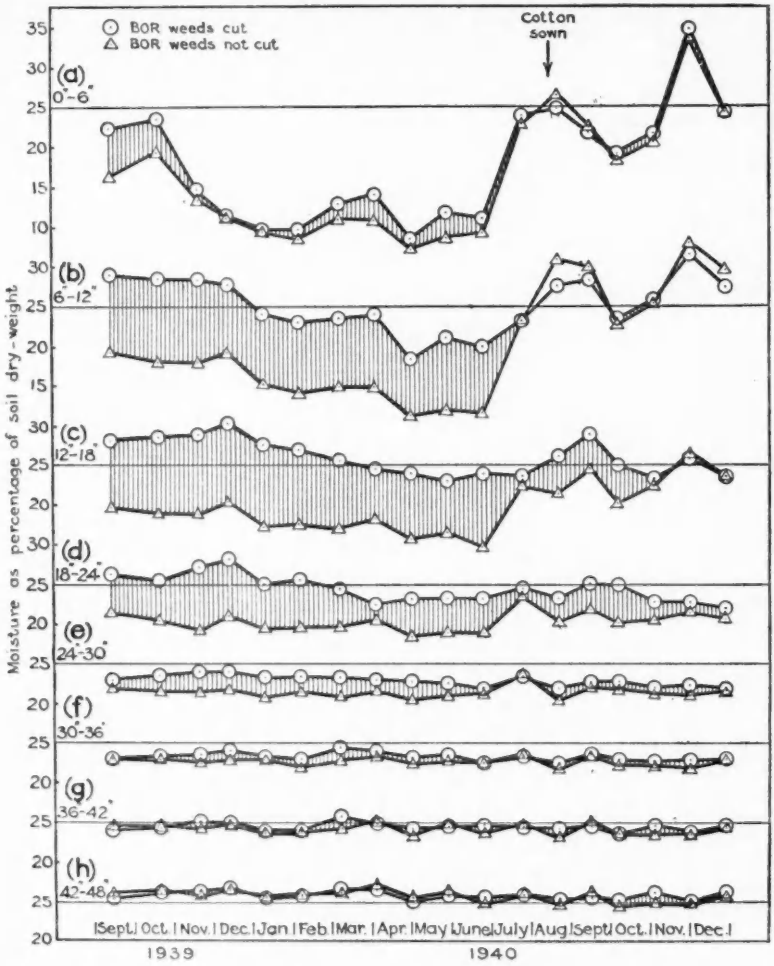

FIG. 3. Effect of weeded and non-weeded bor on soil moisture (for successive 6 in. layers).

the initial hoeing in late August 1939, the weeds[1] were fairly uniformly distributed throughout the plots, shading about 90 per cent. of the whole soil surface. The average weed-height was 10 to 12 in. *Phyllanthus niruri* and *Ocimum basilicum* were dominant, and there was some *Phyllanthus maderaspatensis*. *Dolichos lablab* was also present, being self-sown from a 1938–9 crop of this legume.

It is important to note that the weeds were already well grown before

[1] I am indebted to H. W. B. Barlow, Plant Physiologist, A.R.I., for these observations on weeds.

the first hoeing, so that the comparison is not between clean-weeding and non-weeding of bor, but between (*a*) hoeing the weeds when still green and growing rapidly, and (*b*) leaving them undisturbed to ripen and dry off into a straw-like mass.

After the first hoeing a further total of 5 in. of rain fell that season and any resulting weeds were cut when very small. Meanwhile on the 'normal-practice' treatment the weeds grew to maturity, ripening in October with the drying-out of the upper soil.

The extent of the drain on soil moisture is shown in Fig. 3, which gives monthly moisture-determinations for successive 6-in. layers of the soil of both treatments, to a depth of 4 ft.

The topmost layer of soil under both treatments dried out rapidly through evaporation, and this effectively prevented any further germination of weeds after the rains ceased. In the second and third layers the hoed plots were decidedly moister than the others, at least as early as 2 to 3 weeks after the first hoeing; they remained moister for the following 9 months, until the next rains. The differences were less in the fourth and fifth layers; they were in fact practically confined to the first 2 ft. of soil, being greatest at about a depth of 1 ft.

Very high temperatures are experienced in the 9 months between consecutive rainy seasons. In 1939–40 the mean monthly maximum temperature was never below 92° F. and in April 1940 it reached 107° F. There were also very strong winds and a high saturation-deficit. Despite these highly desiccating conditions the primary factor determining soil moisture 1 ft. below the surface was root-absorption by the weeds of the previous rains. In the absence of roots, either of crop or weeds, the moisture remained in the soil almost indefinitely.

From Fig. 3 it will be seen that plots which were dried out by weeds in 1939 took up more moisture than the weeded ones in the following rains of 1940. It was evident in the field that this greater absorption of water was caused by the much more extensive cracking of the soil on the plots which had previously been weedy and very dry.

Associated with the increases in soil moisture following the hoeing of unripe weeds on the bor, there were considerable increases also in soil nitrates, as shown in Fig. 4. The earliest observations were made in April 1940 and by this time, both in the first and second feet, there was five times as much nitrate in the weeded bor plots as in those where the weeds ripened unchecked. Subsequently the nitrates increased gradually in both treatments until the cotton was sown, treatment differences persisting with little change. When the cotton was irrigated during August 1940 nitrate was leached down from the first to the second foot, and then, as the growing crop absorbed nitrate during September, the amount of nitrate present at both depths fell away, and treatment differences disappeared.

Simultaneously treatment differences became evident in the amount of nitrogen absorbed by the cotton crop. Thus, on September 28, at thinning-time, it was noted that the leaves on the hoed bor plots were darker green than the rest, giving the experiment a chequered appearance.

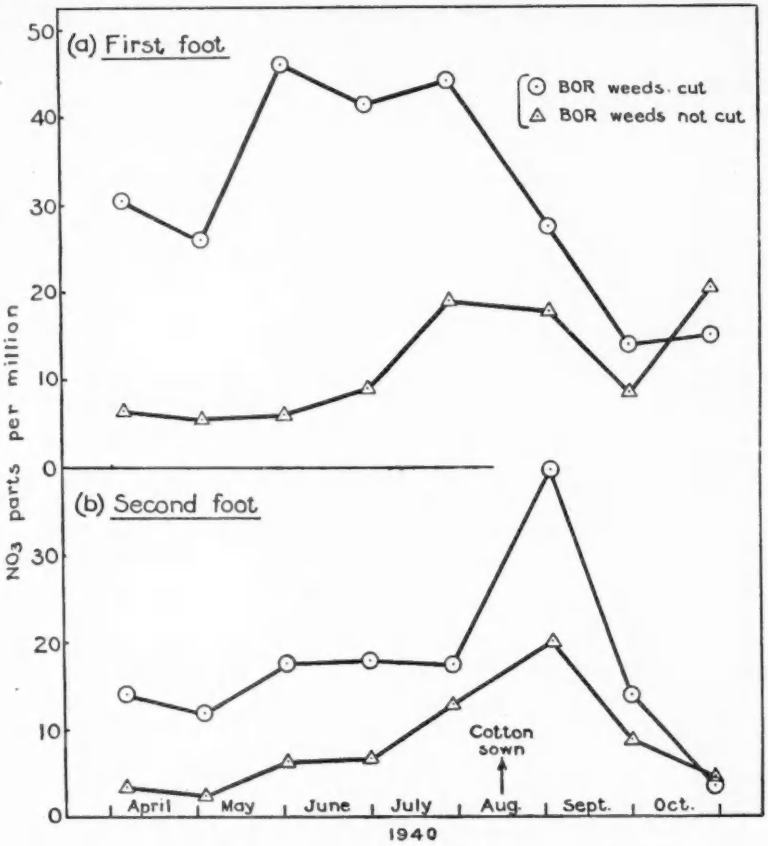

FIG. 4. Effect of weeded and non-weeded bor on soil nitrates.

The mean nitrogen percentages in the cotton leaves during September, expressed on a dry-matter basis were: hoed bor 4·89, unhoed bor 4·71.

From the regression-equations of yield on September nitrogen-percentage mentioned above [4], a difference of this amount between treatments corresponds to a yield-difference of 1·4 kantars per feddan, or about 30 per cent. of the average yield at the Gezira Research Farm.

The additional nitrogen led to increased dry-matter production from October onwards, as is shown in Fig. 5 *a*, which gives leaf dry-weights up to crop harvest. The maximum dry weight was attained in November, and the dry weight of cotton leaves following weeded bor was 65 per cent. greater than that after unweeded bor. The dry-matter curves are of a type resembling those for comparisons of rates of nitrogenous

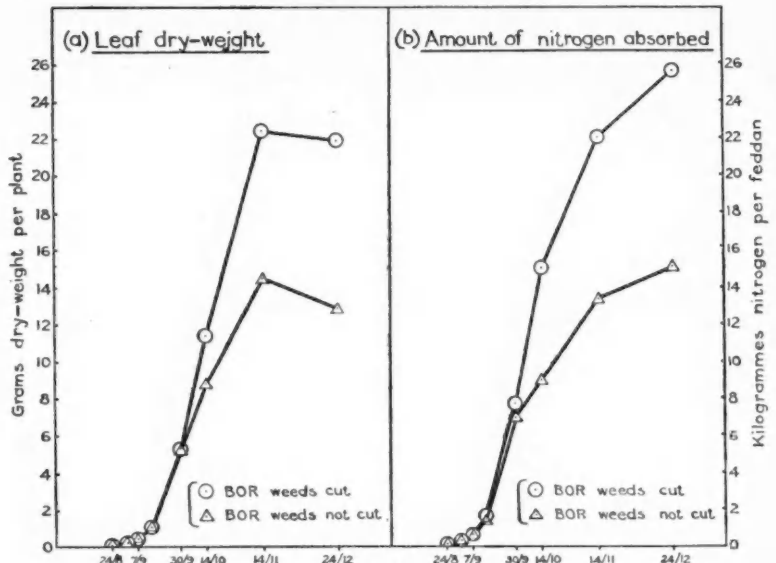

FIG. 5. Effect of weeded and unweeded bor on (*a*) leaf dry-weight, and (*b*) total nitrogen absorption of cotton.

manuring, in which initially all increase at an equal rate but later diverge when nitrogen-supply becomes limiting.

The rates of picking at harvest are shown in Fig. 2 *b*. The total crop obtained, in kantars per feddan, was:

Hoed bor . .	6·18
Unhoed bor . .	4·31
Increase with hoeing	1·87
S.E.	±0·100***

Clean-weeding of the bor from late August onwards increased the yield of the following cotton crop by 43 per cent. The additional nitrogen detected in the data for soil nitrates, and later observed in the analyses of leaf-nitrogen, is reflected, not only in increased dry-weight of the plants, but also in final yield of seed-cotton.

These results accord with those obtained in 1934 in a statistical examination by E. M. Crowther and F. Crowther of rainfall and cotton yields in the Gezira [5]. They found a significant negative correlation between yield and previous year's rainfall. Heavy rainfall means abundant weed-growth on the bor before cotton, and, if the weeds are allowed to ripen, they affect adversely the following cotton crop.

The cotton yields might have increased still more if the bor had been kept entirely free from weeds from the onset of the rains. On the other hand, there may be virtue in allowing young weeds to provide a reservoir of nitrogen in a readily available form, which is liberated when the weeds are cut before maturation.

Discussion

In examining the function of weeds in the Gezira their possible beneficial effect as a protection against soil erosion can be dismissed, since the average slope of the land is less than a foot per mile and the region is subdivided into small units by canals and field-channels. It might, however, be inadvisable, in planning a long-term policy of bor-weeding over a large area, to ignore completely the possibility that the repeated cutting of weeds might slightly increase erosion by increasing soil moisture and therefore surface run-off.

All experimental evidence points to the better nitrogen-supply as the cause of the increased yield through bor-weeding. The total amounts of nitrogen absorbed by the crops of both treatments throughout the season are shown in Fig. 5 *b*. The values refer to aerial parts of the plant only, and are expressed as kg. nitrogen per feddan. The total absorptions up to harvest were:

Hoed bor . .	25·1 kg. N. per feddan
Unhoed bor . .	15·1 ,, ,, ,, ,,
Increase with hoeing	10·0 ,, ,, ,, ,,

The problem of why the amounts absorbed differed to the extent of 10 kg. nitrogen per feddan may be approached from two directions, namely that (*a*) loss of nitrogen occurs when weeds are left unhoed, and (*b*) gain occurs when weeds are hoed.

(*a*) *A Loss of Nitrogen?*

A loss of nitrogen to the cotton crop might be produced through a temporary immobilization of nitrogen in mature weed-residues, accentuating the deficiency already general throughout the Gezira. After the weeds have ripened and seeded unchecked, there remains an abundance of straw-like material which in the dried-out soil fails to decompose until the next rains, i.e., till within a month or two of the cotton-sowing. Thus decomposition may be incomplete when the cotton plants begin to absorb nitrogen, and the amount of nitrogen absorbed may be less in consequence.

If this explanation fitted the present case, and the nitrogen were immobilized only temporarily, it would be expected that the initial depression would be offset later by the effects of the extra nitrogen which became available as the decomposition proceeded. The curves for 'rates of picking' in Fig. 2 *b* should then resemble those of Fig. 2 *a*, where weeds were removed after competing for a period with the young cotton for nitrogen-supply. The curves show no such early depression, but reflect sustained differences in available nitrogen from sowing-time. That such loss of nitrogen to the cotton crop, if loss there be, is more than a mere temporary immobilization is suggested by the yields (rotls per feddan) of a crop of dura (*Sorghum vulgare*) sown on the same land *after* the cotton crop, i.e. in July 1941, and therefore almost two years after the hoeing of the bor-weeds:

	Heads	*Straw*
Hoed bor . .	940·6	4034
Unhoed bor . .	852·5	3409
Increase with hoeing	+ 88·1	+ 625
	S.E. ±37·4	S.E. ±78·4**

The yields of the hoed plots are again higher than those of the unhoed.

Permanent loss by way of the soil is unlikely, for experiments have shown that nitrogen is not readily lost from Gezira soil. Residual effects of ammonium sulphate applied to a cotton crop have been significant for the following cereal crop and even on another cotton crop sown three years after the first.

Any nitrogen lost to the cotton must therefore have previously been absorbed by the weeds. Exactly how this absorption by the weeds could lead to loss is not at present understood. Grazing of the weeds was not responsible, since animals were kept off the experiment. Wind can disperse weeds, but little movement of this kind was observed. Termites provide a possible explanation.

Termites play a role in tropical soils similar to that of earthworms in temperate soils; they move organic matter from the surface down to the subsoil. Termites are numerous and general in Gezira soils, and the abundance of their earth-casts testifies to their activity in breaking down some proportion of the ripe weeds and of crop-residues like cereal-stools. These termites can work in the lower soil layers, fungus-gardens being present at greater depths than those penetrated by the roots of the cotton plant. Determinations of Gezira soil nitrates by Snow and Greene [6] showed very high values for the subsoil, at depths below those usually reached by the roots of the cotton crop, and they mention that termites may be concerned in such nitrate-accumulation. An attractive hypothesis is that termites, which are known to relish a diet of straw-like or woody material, consume the weed-residues and transport them down to their fungus-gardens in the subsoil, where, over a long period, considerable quantities of nitrates may accumulate, to the detriment of the upper soil layers. On this explanation nitrogen would be lost to the surface soil unless seasonal or agricultural conditions encouraged exceptionally deep rooting of the cotton and the consequent tapping of these reserves.

Another suggestion is that nitrogen may be lost during the decomposition of the weed-residues, by reason of the alkalinity of Gezira soil. Jewitt [7] has recently demonstrated that there is considerable loss of gaseous ammonia when ammonium sulphate is applied to this soil, and there seems no reason why gaseous ammonia should not also be liberated during the breaking-down of protein on or near the soil surface.

An explanation based on loss of nitrogen to the cotton through absorption by the weeds is supported by nitrogen analyses of the weeds themselves. The actual weeds of the experiment were not analysed, but weeds growing elsewhere, similar in both vigour and botanical composition, gave an average nitrogen absorption, in the aerial portions, of 10 to 12 kg. per feddan, an amount similar to the difference of 10 kg. per feddan between the amount of nitrogen absorbed by the cotton crop after hoed bor, and that after unhoed bor.

(*b*) *A Gain in Nitrogen?*

The question of a gain in nitrogen when immature weeds are hoed may now be examined. Leguminous weeds can be dismissed, since they

were not represented among the common weeds. Similarly the effect of the previous crop of lubia (*Dolichos lablab*) can be ruled out, since all plots benefited equally, and all received ample rainfall in the heavy 1939 rains to ensure complete decomposition of the lubia-residues, so that they could not exert a critical influence when later the bor dried.

Fixation of atmospheric nitrogen by azotobacter and other agents must be appreciable in the Gezira, or the inhabitants would be unable to maintain their practice of growing rain-dura on the same land year after year. Such dura is meticulously hoed to conserve soil moisture, and there is no parallel with the practice on the irrigated land of leaving the land uncropped during a rainy season, and thus no guidance from native practice as to the treatment of bor-weeds. Rain-dura near Gezira Research Farm yields an average of about 700 rotls grain per feddan, which, with the straw, connotes the removal from the land each year of 8 to 10 kg. nitrogen per feddan. The nitrogen added to the soil through precipitation does not exceed 1 kg. nitrogen per feddan,[1] so nitrogen-fixation in rain-dura land is estimated as at least 7–9 kg. per feddan. This means that the additional nitrogen recovered where bor-weeds are controlled is at least equivalent to the nitrogen fixed in a full year. The only available figure for irrigated land comparable with that of the rain-grown dura is for the 'Continuous Cotton' experiment, which for an average of 23 successive seasons gives an estimated annual removal of 8·4 kg. nitrogen per feddan.

Presumably the primary factor limiting fixation in the arid tropics is soil moisture, and fixation is thus largely confined to the rainy period. Weeds, germinating as soon as the soil is moistened and drawing on reserves of soil moisture (Fig. 3), may greatly reduce the amount of nitrogen fixed per annum. When the land is cropped and irrigated, moisture may still limit nitrogen-fixation, since the desiccating weather conditions following the rainy season lead to marked drying-out of the topmost soil layers between successive irrigations.

From existing data it is impossible to decide whether the differences in cotton yields arise from a loss of nitrogen through unchecked weed-growth or a gain in nitrogen by better nitrogen-fixation through conservation of soil moisture by removal of weeds.

Since in the Gezira Scheme the weeding of bor-land is not practised, the results offer the prospect of a general increase in cotton yields. Hoeing the bor, by conserving soil moisture, restricts soil-cracking, but up to the present, deep and extensive cracking has been deemed essential for maintaining soil aeration and a good tilth. Long-term experiments are needed to show whether the advantage of weeding bor-land is offset by the interference with soil-cracking.

Summary

The paper describes two related experiments investigating the effect of hoeing weeds on the growth and yield of cotton in the Sudan Gezira. In one experiment the weeds grew among the cotton crop, and in the

[1] Unpublished data of O. W. Snow, Soil Chemist, A.R.I.

other on bor (resting) land which did not come under cotton until a complete year afterwards.

The results of the first experiment demonstrated the wisdom of the current practice of clean-weeding from cotton-sowing onwards. Where weeds were allowed to grow unrestrictedly up to 2 months after sowing, the cotton was severely checked in its early growth and final yields were reduced by up to 30 per cent.

In the two treatments of the second experiment, (*a*) the normal practice of allowing weeds on the bor-land, destined for cotton a year later, to ripen and dry off at the end of the rains, was compared with (*b*) cutting the unripe weeds at ground-level while they were still growing rapidly. Cutting the unripe weeds conserved moisture in the soil until the following rains, 8 months later; increased soil nitrates fivefold, and led ultimately to an increase in the yield of the cotton crop by 43 per cent. over that of normal practice. An additional 10 kg. per feddan nitrogen were taken up by the cotton crop when the unripe weeds had been cut a year previously.

Possible agencies are suggested for the cause of this difference, but existing information precludes assessment of their relative importance. Under normal practice termites may cause wastage of nitrogen by removing ripe weeds down to a soil zone untapped by the cotton roots, or ammonia may be lost during the breaking-down of protein in the alkaline soil. Nitrogen-fixation in the soil may be prolonged where moisture is conserved.

Since throughout the Irrigation Scheme the bor-weeds are normally allowed to ripen without interference, the results indicate how a general increase in cotton yields may be attained.

Acknowledgement.—The writer is indebted to the Soil Research Section, A.R.I., for the plant-nitrogen analyses.

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RECENT RESEARCH AT THE DELI TOBACCO EXPERIMENT STATION, MEDAN, SUMATRA

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THE staff of the Deli Tobacco Experiment Station consists of a Director, four departmental chiefs, a secretary, an assistant, an analyst, and sixty natives. It is exclusively concerned with the cultivation of cigar-wrapper tobacco produced from a yearly area of 30,000 acres in a rotation of about eight years (half year tobacco, half year rice, seven years jungle).

The work is divided among four departments, each headed by a specially trained chief: (1) agriculture, (2) botany, (3) entomology, (4) agrochemistry. There is also a department for administration and correspondence that is responsible for meteorological data (particularly rainfall) and a statistical summary of field data (*Bulletin van het Deli Proefstation*).

An account is here given of the results of research work during the last five years or so. They are published in detail in special publications or in annual reports which appear as *Mededeelingen van het Deli Proefstation.*

Agricultural Department (Ir. van der Poel; Dr. Roelofsen)

Manuring.—Fertilizer experiments are made almost exclusively to improve quality, not to increase yields. Although fertilizer experiments have been carried out for half a century, so many new problems are continually cropping up (partly as a result of changes in market requirements) that fertilizing is the chief item on the programme of the Agricultural Department. In the last three years the work has been done by agriculturists engaged by the great tobacco companies.

The normal fertilizing varies with the soil type. Before planting, a mixture of 0–25 gm. of basic slag, 0–2 gm. of K_2O in the form of tobacco-plant ash, and 5–15 gm. of sulphate of potash per plant is broadcast, and 10 gm. of a 5–10–7½ or 5–20–7½ NPK mixture is applied in the planting hole.

It has been demonstrated that a broadcast application of 1·5–2·0 gm. per plant of K_2O in the form of ash a week before planting produces a more uniform and pliant tobacco. This treatment also makes it possible to give more basic slag so as to get a brighter tobacco and larger leaves without the drawbacks of variegated, yellow or reddish coloration, and a too dry and short character. Sulphate of potash has the same effect as ash with the additional advantage that it does not give rise to so moist a tobacco.

It has been found that 20 gm. of basic slag per plant always gives good results on the phosphate-deficient, residual red and black soils, and careful studies are going to be made to determine the optimal doses of slag and ash for the less phosphate-deficient alluvial soils. Since the outbreak of war basic slag has been unobtainable, and experiments have

been initiated to test the value of local sources of phosphate. Pre-war experience had indicated that basic slag was preferable.

Tests on the black dust soils with an additional dressing of P and K after plucking the sand-leaves indicate that the quality of the higher leaves is thereby improved; N is of little or no use.

Variation of the N–P–K ratios of the fertilizer applied in the planting hole has a much greater effect on tobacco quality than variation of the actual quantity applied, or than variation in the earlier fertilizing. At the present time the main object of research is to determine the optimal amounts of P that should be given as guano to different soils.

A fault often observed in the thinnest and finest wrapper leaves is the presence of transparent patches resembling oil stains. Up to the present all attempts to obviate the fault by special (e.g. organic) manuring have been unsuccessful. The method of drying seems to have more influence, the stains appearing at the commencement of drying. Ripe leaves, which dry quickly, are less susceptible than unripe leaves.

The Botanical Department has shown by controlled drying with the aid of salts that slow or irregular drying favours the appearance of these stains. Apart from the impossibility of varying the drying process as applied in present practice, the fact that other qualities are harmed by rapid drying militates against the application of this knowledge.

Some tobacco varieties seem to be fairly immune to the appearance of oily stains.

Slime disease.—Another main line of research of the Agricultural Department concerns the control of slime disease (*Pseudomonas solanacearum*) by cultural means. In pot experiments control was obtained by treatment with gypsum, oilcake, and stabilized humus preparations, but field experiments, with some exceptions, have been unsuccessful. Large applications of well-rotted leaf-mould some weeks before planting were also ineffective.

Slime disease often begins in a root at considerable depth where it is impracticable to apply fertilizer. The uncultivated subsoil may also harbour the disease. No connexion has been found between the structure of the soil and the situation of infected roots.

It is known that the natural jungle-growth harbours the disease, although on a reduced scale, during the seven-year fallow period. The influence of different tree species on the incidence of the disease in the subsequent tobacco plantation has been investigated in a prolonged investigation of regrowth (see *Meded.*, Ser. 3, No. 9). The object is to find the kind of growth that will reduce the disease as much as possible and at the same time give a good-quality tobacco. It has long been known that *Mimosa invisa* controls slime disease, but it has the great disadvantage that tobacco grown after *Mimosa* is of inferior quality. The whole problem of slime sickness, and not only the quality of tobacco, requires investigation by field experiment. It is not sufficient to search for immune plants. The humus-producing and soil-improving properties of the regrowth are just as important as the susceptibility to disease of the plants of which it is composed. It should be noted that shortening the resting period on susceptible land increased the amount

of slime disease in the tobacco. The field experiments, however, last from four to eight years. We are now trying to get results more quickly by letting the plants grow in seed-beds of soil infected with slime disease and determining after one year whether more or fewer diseased seedlings are produced.

It seems possible, by heavy doses of sulphur or of an alkaline fertilizer, to effect such a change in soil reaction that the slime disease in plantations and in seed-beds is greatly reduced or disappears, but this immediately and harmfully influences the growth of the tobacco.

Field experiments.—Statistical treatment of field experiments is not suitable for Sumatra tobacco nor, indeed, for any high-quality product, since a subjective assessment of quality cannot be expressed in figures. In order to get reliable results more quickly from field experiments the advantages and possibilities of modern methods are now being studied.

Botanical Department (Dr. van der Weij)

This department is engaged in physiological, phyto-pathological, and selection studies; the last are limited to selection for disease resistance.

Some recent investigations have concerned the physiology of nutrition in water-cultures. Very well-developed plants are obtained in water-cultures in the open air when the nutrient solution (in 10-litre pots) is changed daily and aerated continuously; as far as we are aware normal plants have not hitherto been obtained in water-culture. With such cultures symptoms of deficiency of the ordinary essential elements N, P, K, Ca, Mg, S, and B in Sumatra tobacco were studied. Deficiencies of N, P, K, and B occur in practice. (See *Bull. D.P.S.*, Ser. 3, No. 44.)

Plant diseases.—Phyto-pathological work has included recent studies of various virus diseases, slime disease, and *Cercospora*.

Control measures against ordinary mosaic have been formulated as a result of extensive investigations (*Meded. D.P.S.*, Ser. 3, Nos. 6 and 11), and it is now possible practically to eliminate the disease which a few years ago was very serious. Primary cases in seed-beds and plantations usually originate from virus in the soil. Badly growing and roughly planted individuals are the most susceptible, and the soil type also affects incidence to a considerable extent. Thorough search for the first symptoms of the disease and direct removal of affected plants are the best ways of preventing infection by contact. The best disinfectant for use by workpeople is a trisodium-phosphate soap solution, but this form of control is of secondary importance. A beginning has been made with resistance-selection against mosaic by crossing with *Ambalema*. The Rotterdam B-virus may also infect tobacco plants from the soil (*Vlugschrift D.P.S.*, No. 61).

Another mosaic disease, formerly often confused with ordinary mosaic and known as *pseudo-mosaic*, does not derive from the soil; it has become important in recent years. It is not readily transmitted by contact and shows such similarity in its way of spreading through plantations to leaf-curl disease which is transmitted by *Bemisia*, that this insect is suspected of being the transmitter. The Entomological Department is, indeed, trying to establish what connexion exists.

In some years frog-eye disease (*Cercospora nicotianae*) causes great damage. Yellow copper oxide, either sprayed or dusted, checks the appearance of white spots and barn spots and is preferable to Bordeaux mixture in that it has no visible effect on the leaf. Unfortunately it may adversely affect the quality of the tobacco, presumably through absorption of traces of copper. Experiments have been made to determine whether very low concentrations can be used. It has been shown that *Cercospora* spores remain virulent for years in the soil of drying-sheds and in harvested tobacco-land. The sub-soil and seven-year fallow land contain few or no virulent spores. No success has attended efforts to isolate less spot-susceptible strains of Sumatra tobacco.

There seem to be greater chances of success in selecting strains less susceptible to slime sickness, the principal disease of Sumatra tobacco. Where tobacco is a quality-product this involves selection not only for disease resistance but also for quality. All foreign tobacco strains are more susceptible than Sumatra tobacco, presumably because in Sumatra, owing to the prevalence of slime disease, there has always been some degree of selection for resistance since tobacco-culture began. From old Sumatra stock several varieties have been selected which displayed high resistance on slime-sick soil, but produced inferior tobacco. From these progeny have been obtained by crossing that seem to possess increased resistance as well as other properties associated with good quality. They are not immune, but the mortality rate is lower, e.g., 20 per cent. against 50 per cent. for ordinary tobacco. Whether this relative immunity persists or not remains to be seen when the produce of selection has been fully tried out in practice.

It is evident, however, that slime disease does not spread from plant to plant through a plantation, and that its patchy occurrence is the result of soil heterogeneity or of seed-bed infection. The disease begins mostly within 18 days after planting (*Meded.*, Ser. 3, No. 10).

Entomological Department (Dr. van der Laan)

Insect pests.—Since Sumatra tobacco produces only wrapper leaf, every small hole caused by any of the many insects that attack the leaf results in an appreciable reduction in value. The chief pests are four caterpillars of the Noctuidae,[1] the capsid *Engitatus tenuis* Reut, and the aphid *Myzus persicae* Sulz. In the tropical climate development is rapid; one generation of *Plusia* is complete in three weeks, of the other caterpillars and of the capsid in a month, and of the aphid in only six days. There is no resting period where there is no marked dry period. During one tobacco plantation, lasting about five months, several generations may develop and often form serious plagues.

Possibilities of control are limited since the tobacco leaf is very sensitive to most chemicals, whilst other insecticides injure the market value of the produce by the formation of film on the leaves. Thus caterpillar damage should be reducible by careful spraying with 1 per cent. lead arsenate solution, but this is only practicable on the seed-bed or on the first-formed leaves in the field, i.e. on leaves that are not harvested.

[1] *Heliothis assulta* Guen, *H. armigera* F., *Plusia signeta* F., *Prodenia litura* L.

The larger tobacco can be protected against *Heliothis* damage in the head only by a careful and sparse dusting with barium fluorsilicate (6–8 per cent.) or lead arsenate (5 per cent.) in the apex. Latterly only the first-named and less poisonous insecticide has been used. In order to get a similar effect a concentration of 8 per cent. (against 5 per cent. for lead arsenate) must be used, and the dusting should be repeated frequently as barium fluorsilicate does not adhere well. The effect is not improved by mixing with flour nor by adding Vatsol OS as adhesive. Cryolite seems practicable; calcium arsenate and Paris green cause too much burning. The contact insecticides derris and pyrethrum have an incomplete effect, as the caterpillars are not very sensitive to them. Chemical methods of control are unsatisfactory against *Plusia* and *Prodenia* since these caterpillars mostly lie underneath the old leaves where they cannot be dusted. These caterpillars and the egg heaps of *Prodenia* are in large measure removed by cheap native labour.

Even after the leaves have been plucked, caterpillars which are three or more days old go on feeding in the drying-sheds, but the younger ones do not. Attempts to kill these caterpillars by brief fumigation of the harvested leaves with HCN, ethylene oxide, ethylene sulphide, or 'methallyl chloride' have failed owing to damage caused to the leaves, or because the fumigant was too impracticable (*Meded. D.P.S.*, Ser. 3, No. 5). Some help is given by dusting with derris, which, however, also damages the tobacco. The best check is to find and destroy the caterpillars before the leaves are hung up.

The source of infection is to be sought in the circumstance that the tobacco plantations are surrounded every year by temporarily abandoned land of former plantations. The chance of a plantation infecting a succeeding one is diminished by the complete removal of all tobacco at the end of the season. This is also the reason why the otherwise harmful *Phthorimaea heliopa* Low. does little damage under these conditions, as it lives exclusively off tobacco. An extensive investigation (*Meded. D.P.S.*, Ser. 3, No. 8) of the life habits of the caterpillars in fallow land showed that they live in certain types of weed vegetation when tobacco is not available. Removal of this vegetation before tobacco-planting time seems to be practicable and economic. As, however, the butterflies seem to have a flying range of several hundred metres, it is not sufficient to keep clear merely the immediate surroundings of the tobacco. Attention is now being paid to the possibility of introducing new parasites of the caterpillars. The *Prodenia*-egg parasite *Telenomus spodopterae* Dodd. has already been imported from Java, but it is not yet known whether it has maintained itself.

Since 1928 the leaf-louse *Myzus persicae* has been sprayed with an aqueous extract of derris root, specially prepared by us. This is now replaced by cheaper and more convenient derris powder, which before use is suspended in water so as to give 0·01 per cent. of rotenone. Much derris spoils the flavour of the tobacco.

Derris, especially for dusting, is also effective against the capsid *Engytatus tenuis* Reut., which bores into the leaf causing weak spots that grow into lesions. Such treatment, however, can only diminish,

not suppress, this pest. Destruction by hand and treatment with pyrethrum and nicotine are ineffective. As in caterpillar control, it is desirable to look out for the host plants of this capsid and to keep them well away from tobacco (*Vlugschrift D.P.S.*, No. 68).

The transmission of pseudo-mosaic has been studied from the entomological point of view with much success. *Bemisia gossypiperda* seems to transmit the virus to tobacco from plants growing on the fallow, especially the Compositae *Eupatorium odoratum*, *Vernonia chinensis*, *Ageratum conyzoides*, *Synedrella nodiflora*, and the Verbenaceae *Stachytarpheta dichotoma*. Owing to neglect of afforestation, *Eupatorium* (symptoms difficult to detect, possibly a symptomless virus carrier) has been able to spread itself freely over several estates, and as a result damage from pseudo-mosaic has attained catastrophic proportions in places. This plant is now eradicated from the jungle. Killing *Bemisia* on the tobacco with contact insecticides, especially pyrethrum-talc dust, is certainly possible, but causes practically no diminution of disease. Keeping *Bemisia* away from tobacco by means of a high fence is more effective, but is still in the test stage. *Bemisiae* are caught from the air on sticky cloth $4\frac{1}{2}$ metres high. It has been shown in practice that they are transported several hundred metres by wind, so that extermination of the plant from a narrow strip in the neighbourhood of the tobacco is not adequate. Attention is now being given to the introduction of new parasites of this insect (see *Vlugschrift D.P.S.*, No. 67).

Nematodes (*Heterodera marioni*) can be very efficiently controlled in seed-beds by fumigation with methallyl chloride, carbon bisulphide, or chloropicrin; the first-named is the cheapest. Seed-taking ants (*Solinopsis geminata*) are killed in the seed-bed by five days' dusting with derris (once daily after the last watering).

At the outbreak of the war the question was being discussed of how to protect tobacco from *Lasioderma* attack. It seemed probable that disinfection with CS_2 would somewhat spoil the flavour, and in order to prevent reinfection after a disinfection the baled tobacco is stored in an insect-free, well-aerated mosquito chamber. The beetles cannot, although their eggs and larvae can, get through the mosquito netting. For this reason the tobacco is nowhere allowed to touch the netting; larvae crawling over the floor are killed with derris scattered on it; larvae falling through the ceiling netting are caught on a sheet of derris-treated cotton. Many hygienic measures are taken to reduce the risk of infection before the tobacco is packed. The damage done by *Lasioderma* has been negligible, thanks to a very restricted use of fumigators.

The principal fumigator now used is the Shell product 'Methallyl chloride', which affects the flavour of tobacco less than does carbon bisulphide, and is more convenient to use on account of its greater insecticidal effect. In the concentration employed it is non-inflammable, and the liquid itself can be made non-inflammable by mixing with $1\frac{1}{4}$ volumes of carbon tetrachloride. Other gases, prussic acid, chloropicrin, methyl bromide, ethylene oxide, were either too dear or did not thoroughly penetrate the closely packed tobacco bales.

Storage in the mountains of Sumatra does not prevent *Lasioderma*

attack. *Lasioderma* is suffocated in the fermenting piles. An impenetrable packing material is useful, but is not completely permeable to air.

In stored tobacco the moth *Setomorpha rutella* sometimes occurs, but does little damage. *Ephestia elutella* is not found at Deli.

In order to guarantee that export tobacco is free from *Lasioderma* attack, control measures and the inspection of stored tobacco are kept in our hands (see *Meded.*, Ser. 3, No. 14).

Agrochemical Department (A. C. Polvliet)

Soil survey.—The extensive agrogeological mapping by Dr. Druif was completed in 1938. A reconnaissance map on a scale of 1:100,000 of the main soil types was prepared. The detailed map (1:5,000) of all soil varieties was nearly finished and only required continuation according to the same criteria as the completed parts. This represents a beautiful and fruitful scientific achievement, of great importance in the evaluation of tobacco soils. For example, all 'red' soils are no longer treated alike, nor are (red) tertiary soils planted, for they produce poor tobacco.

Chemical analysis.—After two years' work based on the agrogeological map a beginning has been made with the collection of agrochemical data. The aim is to be able so to characterize soils by analysis that the results of fertilizer tests on any given soil will give indications of the fertilizer requirements of other soil varieties related thereto not only agrogeologically but also chemically. We are now investigating which analytical methods are the most suitable, i.e. those which give the best agreement with the fertilizer requirements known from experience of the main soil types, and are the most sensitive to the normal fertilizer applications given to tobacco. We have thus come to approve the determination of citric-acid-soluble P_2O_5; carbonic-acid-soluble P_2O_5; K_2O by Morgan's method (acetate buffer, pH 4·8); NO_3 by Morgan's or Harper's method; and pH by the glass electrode.

Analyses of reforested soils which have been under a definite cover for several years have shown that the favourable influence exerted on tobacco by a luxuriant forest-growth is attributable to an increase in P and K. The removal of green material from the forest is harmful, whereas its introduction is beneficial.

We have also investigated whether the composition of tobacco-leaf ash is influenced by fertilizer treatment, in which case ash analyses could be used to give indications of fertilizer requirement. It appears that such an influence does exist, but is by no means simple. An SK application, for example, though it produces better growth, seldom causes an increase in the percentage of K_2O and may cause an increase in SO_3, as well as influencing the content of N and other elements. A rational use of ash analyses in determining fertilizer requirements will be possible only after much experience has been gained in interpreting the figures. The different P and K requirements of the different soil types are reflected in corresponding differences in ash analyses, but here the ash analyses are much less helpful than they would be in comparing

less dissimilar soils. Potash-deficiency is sharply reflected in ash-composition.

An orientated investigation of micro-elements in tobacco and soil was undertaken by us in Holland with the aid of semi-quantitative spectrographic analysis. The tobacco of black soils, which have high P and K requirements, seems to contain relatively little Mn, Zn, Sr, Ba, Ga, and Na. The micro-elements V, Mo, Cu, Co, Cd, Ni, Mn, Al, Ba, Ti, Zr, Ce, Li, Cr, Zn, Pb, and Ga have now been detected in Deli tobacco, besides W, Se, Y, and Cs in the soil.

The Agrochemical Department carries out many kinds of analytical work as well as research in connexion with the control of fertilizers, insecticides, &c.

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THE RELATIVE RESPONSES OF THE POTATO CROP TO DIFFERENT POTASH FERTILIZERS

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NUMEROUS field trials have been made in Great Britain by agricultural research stations, colleges, and county organizers to compare the effects of different potash fertilizers on the potato crop. The objects of these experiments were generally to test the influence of chloride on the potato plant, and to ascertain whether, as cheaper sources of potash, chloride-containing potash fertilizers could be substituted for sulphate of potash without detriment to yield or to quality. This paper is devoted to an examination of the data derived from these comparative experiments. Although farmers are restricted under present circumstances to the use of muriate of potash for potatoes, it is still important to investigate how the food supply of the country may be affected by this particular limitation. Determinations of dry matter or starch-content of the tubers were made at relatively few centres. This is unfortunate, because the relative efficiencies of different potash fertilizers on the potato crop cannot be adequately assessed except in terms of yields per acre of dry matter or starch.

Maskell [1] found that during the later stages of growth of the potato chloride-containing potash fertilizers did not appreciably improve, but sulphate of potash markedly improved, the rate of starch production. He concluded that the superiority of plants treated with sulphate of potash is associated with a more rapid translocation of starch from the leaflets, but does not appear to be wholly due to this fact. The consensus of the experimental results in Germany indicated that sulphate of potash tended to increase, if only slightly, the starch-content of the tubers, but that muriate of potash, and still more kainit, depressed it. In the more recent experiments on the Continent, such as those by Opitz [2], Berkner [3], and Nemec [4], it has been the rule to state the results of comparative potash trials in terms of yields of tubers as well as of starch per acre; assessed by the latter standard, sulphate of potash has generally proved superior to the chloride-containing potash fertilizers. Odland [5] found in prolonged tests at Rhode Island that kainit, muriate of potash, and sulphate of potash were equally effective sources of potash on potatoes, but the basis of comparison appeared to be tuber-yields per acre. Vinogradsky [6] found that muriate of potash reduced, and sulphate of potash increased, the starch-content. Tamman [7] concluded that sylvinite caused significant falls in yield and starch-content and that all potash fertilizers tended to reduce starch-content. Russell and Garner [8], by an analysis of the experiments at Rothamsted, Woburn, and other centres, showed that the chloride depressed the yield of tubers.

The present survey deals with 186 comparative experiments in Great

Britain. These were carried out in divers parts of the kingdom and cover a wide range of seasons and of soil types mostly belonging to the light-texture class. Practically all the experiments studied were designed to compare chloride-free sulphate of potash with chloride-containing potash fertilizers, muriate of potash, and a low-grade salt (kainit or sylvinite).

The old 'kainits' generally contained varying amounts of magnesium sulphate, but the 'kainits' chiefly imported in recent normal years were of the sylvinite type, and practically free from magnesia. The available evidence, however, indicates that magnesium sulphate has no marked beneficial or deleterious effect on the potato crop in this country. Thus the essential difference between muriate of potash and kainit or sylvinite is related to the sodium-chloride content, which amounted to about 15 per cent. in the former as compared with 45 to 60 per cent. in the latter. Moreover sodium has not been found to affect appreciably the potato crop; so the differences in response to the three potash fertilizers would have been due mainly to differences in the levels of chlorine applied, approximately in the ratios 0, 1, 4, after adjustment of the respective potash-fertilizer dressings to furnish equal weights of potash (K_2O) per acre. Most of the experiments were of the old single-plot or old replicated type; the more recent Rothamsted and Woburn experiments were of the modern factorial design. The experiments have been grouped into two classes according to the presence or absence of control treatments without potash (NP). In the former the results are expressed in terms of potash responses, and in the latter in terms of responses to complete artificials varying in their source of potash. As the quantities of potash tested per acre varied with the experiments, the potash responses and the response-differences between the potash fertilizers, for the sake of a better comparison, have been converted to responses to a standard dressing of 0·5 cwt. K_2O per acre by the use of the appropriate factor in the Crowther and Yates table [8].

TABLE 1. *Responses of the Potato Crop to Different Potash Fertilizers*

	Mean responses to potash—Tons/acre			*Diff. as compared with sulph. potash*	
	Sulph. pot. 0·5 cwt. K_2O No Cl	*Mur. pot.* 0·5 cwt. K_2O 0·5 ,, Cl	*Kainit* 0·5 cwt. K_2O 2·0 ,, Cl	*Mur. pot.*	*Kainit*
No dung . .	2·00	1·95	1·36	−0·05	−0·64
(63 trials)	S.E. ±0·216	S.E. ±0·260	S.E. ±0·210	S.E. ±0·09	S.E. ±0·16
With dung .	0·57	0·43	0·12	−0·14	−0·45
(61 trials)	S.E. ±0·12	S.E. ±0·131	S.E. ±0·141	S.E. ±0·093	S.E. ±0·105

Both with and without dung the decrease in the response to muriate of potash is not significant, but the decrease by kainit is highly significant. The evidence suggests that dung ameliorates slightly the effect of chlorine on the yield.

Table 2 summarizes the comparative experiments, which included no

control treatment (NP), and gives the results in terms of mean responses to complete artificials (complete artificials—no artificials):

TABLE 2. *Responses of the Potato Crop to Complete Fertilizers*

	Mean responses to complete artificials Tons/Acre			*Diff. as compared with sulph. potash*	
	Sulph. pot.	*Mur. pot.*	*Kainit*	*Mur. pot.*	*Kainit*
No dung (45 trials)	3·08	2·84	2·39	−0·17 S.E. ±0·09	−0·49 S.E. ±0·13
With dung (17 trials)	1·16	1·43	1·08	+0·21 S.E. ±0·16	−0·07 S.E. ±0·20

It is interesting to note that the average of sulphate and muriate of potash series, viz. 2·96 tons, agrees tolerably well with the sum of the mean responses in Great Britain to nitrogen (0·25 cwt.), phosphoric acid (0·5 cwt.), and potash (0·5 cwt.), viz. 3·14 tons, published by Crowther and Yates [9]. The latter figure, of course, does not contain effects due to interactions.

Muriate of potash has not significantly depressed the yield, as compared with sulphate of potash, but the depression due to kainit is again marked and highly significant. With dung, on the other hand, the differences between the potash fertilizers are not statistically significant. The data suggest that dung levels up the effects of the potash fertilizers, but the number of experiments in this group is too small to warrant positive conclusions.

The reductions in yield caused by muriate of potash and kainit respectively, compared with the return from sulphate of potash, have been calculated from the data given in Tables 1 and 2, as follows:

TABLE 3. *Reduction in Yield of Potatoes caused by Muriate of Potash and Kainit*

Mean reductions in yield of tubers as compared with sulph. pot.				
	Mur. pot. 0·5 cwt. K_2O 0·5 ,, Cl	*S.E.*	*Kainit* 0·5 cwt. K_2O 2·0 ,, Cl	*S.E.*
	cwt./acre		cwt./acre	
No dung (108 trials)	2·0	±1·81	11·6	±2·83
With dung (78 trials)	1·2	±1·08	7·2	±1·86

The mean decreases in yield are not statistically significant. The mean depressions by kainit, on the other hand, are highly significant. In 186 experiments with and without dung the mean depressions due to 1 cwt. muriate of potash and to the equivalent weight of kainit are 1·67 cwt. and 9·81 cwt., respectively. These decreases, when assessed by the quantity of chlorine applied, are equivalent to a mean depression of 4·40 cwt. potatoes by 1 cwt. chlorine. This figure is in substantial agreement with the decrease of 5 cwt. potatoes estimated by Russell and

Garner [8] to result on the average from 2 cwt. muriate of potash, as compared with the return from sulphate of potash.

As more than 80 per cent. of the trials were conducted on light soils, the data afford little scope for examining the relative reactions of light and heavy soils to chloride-containing potash fertilizers. The largest number of trials in the same area and embracing nearly an equal number of light and medium-heavy soils was carried out in the north of England. The mean decreases in yield from chlorine in these respective soil groups were:

	No. of experiments	*Decrease in yield by 1 cwt. Cl*
North of England		
Light soils	25	4·2 cwt. potatoes
Medium-heavy soils	22	5·5 ,, ,,

The results suggest that the depression of the yield by chlorine is not significantly affected by differences in soil texture.

Examination of the data indicates that the adverse effects of chlorine on yield are proportionately greater with large than with small quantities. It would appear that the potato plant, from the point of view of yield, is little affected by small concentrations of chlorine in the soil below a certain critical level. Observations have shown that chloride-containing potash fertilizers tend to produce light-coloured foliage and earlier death of the haulms. These effects were consistently marked on the kainit plots, but they were not strongly characteristic of treatment with muriate of potash in certain seasons. These observational data suggest that the harmful influence of the chloride ion may be due to its effect in curtailing the growth-period and preventing the full maturity of the crop.

A review of the detailed data reveals that, as compared with sulphate of potash, smaller yields have resulted from muriate of potash in 62 per cent. and from kainit in 85 per cent. of the experiments. In presence of dung the results were not appreciably altered, showing 58 per cent. of yield-reductions from muriate of potash and 78 per cent. from kainit.

Examination of the distribution of the experiments does not reveal, as might have been expected, a general inverse relation between chlorine effects and the mean annual rainfall for different localities. Two wet regions, north-west England and south-west Scotland, are characterized by considerable depressions in yield due to chlorine. On the other hand, certain districts with lower rainfalls, south-east England, north-east and south-east Scotland, show small chlorine effects, one or two being actually positive. Other relatively low-rainfall areas, such as the East Midlands and north-east England exhibit marked decreases in yield by chlorine. The vital factor in reducing the amount of injury by chlorine may be adequate seasonal rainfall, after application of the fertilizers, to wash most of the chlorine out of the soil before it gains access to the plant in toxic quantities. This is borne out by the much smaller effects of chlorine in the Scottish experiments in 1899, when the rainfall in May was more than twice the normal for the month, as compared with 1900, when the rainfall in the same month was approximately normal. The occurrence of mean positive responses to chlorine in a few regions of lower rainfall indicates that a small quantity of chlorine may actually

stimulate growth of the potato plant in dry conditions. This is also indicated by the marked proportion of trials where muriate of potash has given larger yields than sulphate of potash.

Effect of Potash Fertilizers on Composition of Potatoes

Determinations were made of dry matter in the tubers in 42 trials without dung and 21 trials with dung. The quantity of potash tested without dung was 1 cwt. K_2O per acre, involving the application of 1 cwt. chlorine in the form of muriate of potash and 4 cwt. chlorine in the form of kainit. In the trials with dung the quantity of potash tested per acre was 0·75 cwt. K_2O with an accompanying supply of 0·75 cwt. Cl and 3 cwt. Cl in muriate of potash and kainit, respectively. Table 4 summarizes the dry-matter contents of tubers at the centres where the experiments were extended to study this aspect of the problem.

TABLE 4. *Relative Effects of Potash Fertilizers on Dry-matter Contents of Tubers*

	Mean percentages of dry matter in tubers from complete fertilizers			*Difference in dry matter per cent. as compared with sulph. pot.*	
	Sulph. pot.	*Mur. pot.*	*Kainit*	*Mur. pot.*	*Kainit*
Scotland—Central, SW., and SE. 1899 and 1900					
No dung (21 trials) . .	24·80	23·24	21·80	−1·56 S.E.±0·25	−3·00 S.E.±0·33
With dung (21 trials) . .	24·12	22·97	22·05	−1·15 S.E.±0·30	−2·07 S.E.±0·29
North of England, 1900–2					
No dung (16 trials) . . .	24·33	23·19	22·12	−1·14 S.E.±0·25	−2·21 S.E.±0·41
Miscellaneous centres in England No dung					
Rothamsted, Herts. 1922 . .	24·26	22·02	19·68	−2·24	−4·58
,, ,, 1923 . .	21·73	20·85	17·87	−0·88	−3·86
Reaseheath, Cheshire 1922 .	21·68	19·63	17·28	−2·05	−4·40
Seale Hayne, Devon 1922 .	24·40	22·30	22·70	−2·10	−1·70
Usk, Mon. 1923 . . .	23·60	22·50	21·00	−1·10	−2·60
Mean for miscellaneous centres .	..	..	..	−1·67	−3·42
General mean for Great Britain: (42 trials)	..	..	..	−1·41	−2·74
No dung	..	..	..	S.E.±0·16	S.E.±0·24

The detailed data indicate that both muriate of potash and kainit depressed the dry-matter content of the tubers in each experiment. It is also noteworthy that the mean depression in each set of trials by kainit is approximately twice that produced by muriate of potash. The smaller chlorine effect with dung in the Scottish trials is consistent with the reduced application of chlorine and is not necessarily due to the counteracting influence of the dung.

The above results suggest that the depressive effect of chlorine on dry matter is proportionately greater at the lower level of application (1 cwt. Cl per acre) than at the higher level (4 cwt. Cl per acre). It may not be possible to explain this result until the mechanism of the action of chlorine on the plant has been elucidated. After adjustment of the results to the quantities of chlorine applied, the figures do not indicate an appreciable effect of dung in reducing the effect of chlorine on the dry-matter content.

At certain centres estimations were also made of the starch-content of the tubers from the different plots. The values for starch have been related to the dry-matter content and crop yields per acre; the results are summarized in Table 5.

TABLE 5. *Relative Effects of Fertilizers on the Starch-content and Yield of Potatoes*

Centres	*Mean Values*			
	Yield in tons of tubers per acre	*Dry matter in tubers per cent.*	*Starch in dry matter per cent.*	*Starch tons per acre*
Scotland				
No dung (21 trials):				
Sulph. pot. . . .	7·30	24·80	80·56	1·45
Mur. pot. . . .	6·88	23·24	79·63	1·27
Kainit	6·49	21·80	79·61	1·13
Differences as compared with sulph. pot.:				
Mur. pot. . . .	−0·42	−1·56	−0·93	−0·18
	S.E. ±0·12	S.E. ±0·25	S.E. ±0·25	S.E. ±0·024
Kainit	−0·81	−3·00	−0·95	−0·32
	S.E. ±0·22	S.E. ±0·33	S.E. ±0·19	S.E. ±0·05
With dung (21 trials):				
Sulph. pot. . . .	7·26	24·12	80·19	1·40
Mur. pot. . . .	7·42	22·97	79·87	1·37
Kainit	7·06	22·05	79·59	1·25
Differences as compared with sulph. pot.:				
Mur. pot. . . .	+0·16	−1·15	−0·32	−0·03
	S.E. ±0·21	S.E. ±0·30	S.E. ±0·15	S.E. ±0·05
Kainit	−0·20	−2·07	−0·60	−0·16
	S.E. ±0·23	S.E. ±0·29	S.E. ±0·17	S.E. ±0·05
Rothamsted				
Sulph. pot. . . .	8·30	24·26	65·84	1·325
Mur. pot. . . .	8·32	22·02	64·00	1·175
Kainit	8·06	19·68	58·20	0·925
No potash . . .	2·47	23·07	57·16	0·325
Differences as compared with sulph. pot.:				
Mur. pot. . . .	+0·02	−2·24	−1·84	−0·15
Kainit	−0·24	−4·58	−7·64	−0·40

The above data indicate that the chloride-containing potash fertilizers reduced not only the dry matter of the tubers but also the percentage

of starch in the dry matter. The mean depressions of starch in dry matter by the muriate and kainit, as compared with sulphate of potash, are appreciable and statistically significant, except with the muriate in presence of dung. The mean depression of starch in dry matter by the muriate in 21 trials without dung is 0·93 per cent. The adjusted figures do not reveal that dung has much influence on the effect of chlorine on starch-content. The Rothamsted results further show that, as compared with no potash, sulphate of potash has not reduced the dry-matter content, but muriate of potash and especially kainit have markedly depressed it. The cumulative data from all the relevant experiments demonstrate the importance of assessing the effectiveness of potash fertilizers on the potato crop in terms of starch or, at least, of dry-matter production per acre. Crowther [10] has shown that potash has no effect on the nitrogen-content of the dry tubers.

The dry-matter content of potato tubers has also been studied in relation to the rainfall and general manuring. A comparison of this kind is possible only where similar conditions in regard to soils, manuring, and variety of potato are maintained within the same series of experiments. The results are summarized in Table 6.

TABLE 6. *Relative Effects of Rainfall and General Manuring on Dry Matter in Tubers*

Centres	*Dry matter in tubers*	*Rainfall Apr.–Sept. incl.*
North of England:	*Per cent.*	*Inches*
Mean of 5 tests: Nil	23·7	
KPN (sulph. pot.)	23·4	15·0
Mean of 5 tests: Nil	25·6	
KPN (sulph. pot.)	25·2	12·3
Mean of 6 tests: Nil	..	
KPN (sulph. pot.)	24·4	12·5
Scotland: central		
Mean of 9 tests: Nil	25·4	
KPN (sulph. pot.)	25·4	
Dung only (10 tons)	24·9	11·9
KPN (sulph. pot.) with dung	24·9	
Dung only (20 tons)	24·2	
Mean of all treatments	25·0	
Scotland: south-east		
Mean of 7 tests: Nil	25·7	
KPN (sulph. pot.)	26·8	
Dung only (10 tons)	24·4	12·1
Mean of KPN plots (sulph. pot.) with dung	25·4	
Dung only (20 tons)	24·2	
Mean of all treatments	25·3	
Scotland: south-west		
Mean of 5 tests: Nil	20·4	
KPN (sulph. pot.)	21·0	
Dung only (10 tons)	21·1	19·0
KPN (sulph. pot.) with dung	20·7	
Dung only (20 tons)	21·5	
Mean of all treatments	20·9	

The above data indicate a general inverse relationship between the dry-matter content of potatoes and rainfall in the months April–September in each territory. This is only in accordance with expectations. The higher levels of dry matter in the tubers, viz. 24–26 per cent., appear to be associated with approximately 12 in. of rainfall in the months in question. The evidence also shows that the conventional dressing of complete artificials, using sulphate of potash as a source of potash, has but slightly affected the dry-matter content of the tubers, reducing it in the Scottish experiments by 0·46 per cent. without dung and by 0·31 per cent. with dung. In north England the mean depression by complete artificials without dung is 0·36 per cent. Similarly, treatment with 10 tons of dung only per acre has had little effect on the dry matter of the tubers, the average depression in 21 experiments being 0·53 per cent. as compared with no treatment. On the other hand, the use of 20 tons dung per acre has significantly decreased the mean dry-matter content of the tubers by 1·0 per cent.

Effect of Different Potash Fertilizers on the Cooking Quality of Potatoes

The evidence from the comparative experiments, which involved testing of the cooking qualities of the tubers grown with different potash fertilizers, is not consistent except in one or two features. The data generally agree that the use of kainit leads to the production of poor cooking potatoes, which are soapy in texture and tend to blacken after boiling. This was the evidence from the north of England tests [11], which revealed little difference between potatoes grown with sulphate of potash and muriate of potash. In a later investigation Wheldon [12] found that with dung the potatoes grown with sulphate of potash were superior in colour, texture, and flavour to those grown with muriate of potash or kainit.

The data from the Scottish experiments [13], on the other hand, reveal tolerably consistent differences in presence of dung but not in its absence. Where no dung was used, the potatoes grown with sulphate of potash were judged the best in 9 out of 12 experiments, as compared with 2 out of 12 experiments with muriate of potash. In presence of dung, however, potatoes that received sulphate of potash were judged best in only 4 experiments out of 12, as compared with 2 out of 12 with muriate of potash, and 3 out of 12 with no treatment. Kainit produced the worst potatoes in 9 trials out of 12, without dung, as against 7 trials out of 12 with dung. The evidence thus indicates that dung had a levelling-up effect, especially with smaller quantities of chlorine as supplied by muriate of potash. In later investigations at Craibstone, Aberdeen, Findlay [14] found little difference between sulphate and muriate of potash in dry seasons, but in seasons of greater rainfall the sulphate was distinctly superior and the colour of the potatoes when boiled was better. The low-grade potash fertilizers were distinctly the poorest and a large number of the tubers turned black, especially in wet seasons.

The evidence from experiments at Kirton, Lincoln [15], also bears out the superior quality of potatoes grown with sulphate of potash, especially

as compared with those from no-potash treatment. This evidence assigns to muriate of potash a cooking quality about midway between the two. The low-grade salts have always produced tubers of rather poor quality.

The Rothamsted data [16] on the cooking quality of potatoes from experiments carried out in 1929 indicate that chipped potatoes were not uniformly affected either in colour, flavour, or consistency by potash fertilizers, but boiled potatoes were improved in colour by potash fertilizers. Muriate of potash gave the best results, sulphate came second, and potash salt third. For flavour the potash fertilizers came out in the same order, but only the best of the samples were equal to those grown without potash and the others were inferior. It was generally concluded that the effects of fertilizers were small by comparison with the effects of different soils.

In cooking tests on potatoes from an experiment carried out with dung by the Berkshire Agricultural Committee [17] the marks given the cooked potatoes were 83 for muriate of potash, 78 for sulphate of potash, 81 for kainit, and 72 for no treatment, in each case 100 being maximum marks.

Despite frequent assertions by practical growers that they have found potatoes grown with muriate of potash to turn black after cooking, the official comparative tests do not support the evidence. The writer [18] has shown that grey to black discoloration of potatoes after boiling is induced by potash deficiency, in combination with a relatively high nitrogen level in the soil. It has been clearly established that kainit does lead to the production of potatoes with a strong tendency to boil black. It is possible that muriate of potash may cause a certain degree of discoloration in certain conditions, depending on seasonal rainfall and on the quantity applied per acre. Under present circumstances when muriate of potash dressings are restricted to a relatively low level the risk of such effects being produced is small.

Summary

Examination is made of the available data from 186 experiments comparing the effects of chloride-free and chloride-containing potash fertilizers on the potato crop.

The data indicate that, as compared with sulphate of potash, the mean decreases in yield of tubers per acre from 1 cwt. muriate of potash are 2·0 cwt. without dung and 1·2 cwt. with dung. In neither case is the reduction significant. On the other hand, the mean reductions by an equivalent dressing of kainit are highly significant, being 11·6 cwt. without dung and 7·2 cwt. with dung. The results also show that the use of dung ameliorates the harmful effect of chlorine on yield. The mean depressions in the dung and no-dung experiments are 1·7 cwt. from muriate of potash and 9·8 cwt. from kainit.

The analytical data show that muriate of potash and kainit depress the dry-matter content of the tubers. The mean reduction in 42 trials is 1·41 per cent. from muriate of potash and 2·74 per cent. from kainit, both reductions being highly significant. The data further indicate that dung does not appreciably reduce the effect of chlorine on the dry

matter of the tubers. The percentage of starch in the dry matter is also depressed by the chloride-containing potash fertilizers.

Further examination of the results has revealed a general inverse relationship between rainfall and dry-matter content of the tubers.

Conventional dressings of complete artificials or moderate dressings of dung, 10 to 12 tons per acre, do not significantly reduce the dry matter of the tubers, but the use of 20 tons dung significantly depressed the dry matter by 1 per cent.

The evidence indicates that kainit leads under certain conditions to the production of potatoes with a soapy texture and a tendency to blacken after boiling. The data are not consistent in respect of differences in cooked quality between sulphate and muriate of potash.

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STEM-GIRTH AS A CRITERION IN FIELD TRIALS WITH YOUNG CLOVE TREES

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Introduction.—The clove tree (*Eugenia caryophyllata*), of which the unopened buds are the harvested produce, does not normally bear until the fifth or sixth year, and it is not until several years later that the bearing settles down sufficiently for reliable figures to be taken in yield trials. Furthermore, the adult tree bears most irregularly, sometimes in alternate years, or often at less regular intervals. Attempts have been made to find a regular cycle of bearing, but these attempts, so far, have failed, and at present yields in field trials must be taken over several years before adequate data are obtained on which to base experimental results.

Experimental work with the clove is therefore prolix, and trials in the establishment of seedlings in the field may make very slow progress. Moreover, such establishment trials are usually of an exploratory nature, as the results and experience gained in one trial frequently lead to the laying down of another.

These considerations have led to the search for physical characters which can be easily measured in the pre-bearing stage, and which are correlated with yield. Such a character could probably be used to obtain quicker results in establishment trials.

It may be mentioned that contemporary legislation in the Zanzibar Protectorate, which has involved the Government in taking over the mortgages on some thousands of clove estates, after careful valuation, has also stimulated the search for an easily measurable physical characteristic of the clove tree which is indicative of yield capability. As will be shown below, this need was in part met by estimating age and relative canopy, but this measure was not exact enough for the assessment of vigour in experimental blocks of trees of one age.

Although recording work to this end has been in progress in Zanzibar for several years, the amount of the available data is still regrettably small. This is due to the block of 600 mature trees, on which the adult-tree side of the investigation depended, losing half its component trees in the 'sudden death' condition, whilst practically all the blocks of young seedlings established in earlier years have been so thinned by the depredations of termites as to make the bulk of them statistically useless. As a result of the partial failures of establishment trials in this manner, methods for the successful establishment of young cloves are slowly developing. A record of such correlations as have been established may be of value, however, in view of a possible analogy with other tree crops.

Relative Canopy

The greater part of the earlier work was done by Wigg [1], whose unpublished data enabled the clove-estate valuations for legislative purposes to be based on scientific evidence. Wigg indicated that whereas stem-girth, height, and canopy were all correlated with yield, canopy

was a character that could be measured with speed and accuracy, and when applied to a series of classes based on age could be used to assess the bearing capacity of whole estates of mixed types of clove trees. Wigg describes the meaning and assessment of canopy as follows:

When a tree is classified for canopy, the complete cylindrical form with foliage down to the ground is kept in mind. This latter would be an 8/8 tree. Deductions are then made for all deficiencies in the canopy by imagining the telescoping of the foliage into the upper part of the tree so that above a certain point on the tree the canopy would be full and below it there would be none. The canopy class is then got by a straight ratio of this imaginary vertical length to total height. Suppose a tree to be forty feet high and that it is estimated that there is sufficiently leafy covering (if it were compacted in a full distribution into the upper part of the tree) to clothe in full distribution 5/8 of the length of the tree, the canopy class would be 5/8. If in this case the only deficiency were in the lowest part of the tree the actual vertical crown length would be 5/8 of 40 feet or 25 feet, the lower 15 feet carrying no foliage. . . . The actual height is not considered in this, only the relative length that carries the full complement of foliage, but in booking the entries (which are marked in position as the planted pickets) symbols are used to indicate blanks, seedlings, saplings, poles, mature and over mature trees. . . . The obvious importance of the amount of foliage of the clove tree lies in the manner in which the inflorescences are borne. The foliage is made up of the leaf-equipment of the seasonal shoots, which are carried at the ends of the branches. Although the clove is evergreen, large quantities of leaves are continually being shed particularly in dry periods so that it is at the most only the last three sections which generally carry leaves. The leaf-equipment of each seasonal shoot is directly concerned in the elaboration of materials for the production of the terminal inflorescences which they bear when crop is produced. When a tree is in full crop the whole crown is covered with inflorescences; probably up to ninety per cent. of the terminals carrying inflorescences. The more leafy the twigs, therefore, the more equipment there is for the production of crop, and more definitely where there are no leafy shoots there will be no production of crop.

It is clear from the above that the measurement of canopy is a relative measure and even when subdivided into the six age-groups that Wigg used is still a measure relative to the type of tree under consideration. Thus a full-canopied tree of the mature class could be more or less of any size and quality so long as the tree has reached the required age, and was fully equipped with leafy twigs. It might be 20 or 50 ft. high. In valuation procedure, of course, this fact was borne in mind by the valuer, who applied an actual cash correction accordingly. However, the fact that within a group homogeneous for age and roughly for size the character of canopy is correlated with yield is shown by the following figures obtained by Wigg from the 600-tree block mentioned above.

Correlation between Canopy and Yield.—(The canopies were measured in eighths of a full canopy and yields in pounds of dried cloves per season. The yield figures were averages of four seasons' harvests.)

Population	*No. of trees*	*Correlation coefficient*
1. Whole population ignoring heights	447	+0·364
2. 'Forty-foot' class, trees 36–45 ft.	182	+0·4159
3. 'Thirty-foot' class, trees 26–35 ft.	263	+0·257
4. Class of 36–40 ft.	158	+0·4096
5. Class of 31–35 ft.	237	+0·255

All these coefficients of correlation are significant at $P = 0{\cdot}01$ point. That the expression 'whole population ignoring heights' be not misunderstood it should be realized that these figures refer to a block of clove trees that are reasonably uniform in appearance. Moreover, the array for 'canopy classes' contains no representatives of one-eighth and eight-eighths canopies and only one for the two-eighths class.

Nevertheless, the criterion of relative canopy may be considered not entirely suitable for experimental work as the eight classes afford too rough a measure for detailed work, and visual classification into more canopy classes than eight would be not only very difficult but liable to error both by wrong assessment and by the personal idiosyncrasies of the observer. Thus it is not unusual for two observers to disagree in a classification based on eighths, so that disagreement would be inevitable in a more exact subdivision of the full canopy.

Furthermore, whereas a canopy survey is not difficult with mature trees which do approximate in shape to Wigg's 'leafy cylinder', a young tree of 2–5 years of age is difficult to assess and approximates more to a cone in shape than to a cylinder.

Stem-girth

Stem-measurements, either as trunk circumference or cross-sectional areas, have long been held to be useful indicators of tree vigour. Anthony and Sudds [2] showed that with apples a high correlation existed between girth-measurements and yield, and held that such measurements alone would suffice in studies of apple-tree vigour. Wigg also indicated a similar relationship with cloves.

(*a*) *Correlation of girth and yield in mature trees.*—One of the factors which has hitherto made difficult the measurement of clove-tree girths is that the mature tree tends to branch low down on the main stem, so that if a single measurement of girth is required, it must be taken so low on the trunk that the swellings due to the upper roots render girth-measurement very inaccurate. In the work described below this difficulty was overcome by taking the individual measurements of all stems and branches at a given height and converting these several figures into one representing the supposed girth had the tree a single stem only. The single figure was the square root of the sum of the squares of the component branches. This enabled the girths of all the existing trees in the 600-tree block to be measured at a height of 3 ft. from the ground and a correlation to be calculated between these figures and the average yield of these trees based on the previous seven-years records. These figures yielded a significant positive correlation coefficient of 0·357 for 349 trees.

(*b*) *Correlation of girth and canopy area in young trees.*—These trees are, however, fully mature; with the exception of subsequent replacements they were planted about 1875. The existence of a relationship between girth and yield having been proved, it became necessary to obtain similar evidence for younger trees, as this would satisfy one of the main experimental needs.

As shown above, the yield of a clove tree of any age must be largely

governed by the foliage-equipment, for not only does the evergreen canopy control the photosynthetic activity of the tree, but the actual cloves are borne on the terminals of the leafy shoots. An attempt was, therefore, made to measure, not the relative canopy used by Wigg, but the actual canopy in square feet for a block of young trees. This was done by assuming that the geometric shape nearest to that of the young tree is a cone. The area of the surface of a cone minus the base is half the product of the basal circumference and the length of the slope. For each tree the area calculated in this way from actual measurements was reduced by multiplying by the relative canopy in order to allow for imperfections in the leafy equipment of the tree. Thus

$$\frac{L \times C}{2} \times \frac{\text{canopy}}{8},$$

where L = length of slope and

C = basal circumference, both in feet.

The resulting figures for 357 seven-year-old clove saplings indicate their actual leaf-bearing surface-area in square feet. These figures were then correlated with girth as indicated by stem-circumference in inches measured at 4 in. from the ground. (The girth-measurement has to be made near the ground in a young tree as measurements at 3 ft. would involve the examination of several score of branches of less than 1 in. circumference.) This works out at the highly significant positive co-efficient of 0·79 for 357 trees.

(*c*) *Correlation of yield and girth of mature trees corrected for canopy.*—This close relationship between girth and actual canopy in young cloves indicated a method of improving the established correlation between girth and yield in mature trees. The variations in this relationship are mainly caused by reduction in the canopy of mature trees either by disease or by mechanical damage due to the breaking of branches during picking. Thus a tree of large girth and associated large actual canopy might have a large portion of the canopy broken away, resulting in the yield being reduced to a figure much lower than might be expected for a tree of such a girth. As mature trees could not readily be measured for surface-area, a method consisting of the multiplication of the girth-measurement by the fraction representative of relative canopy was attempted. Thus a tree with a girth of 50 in. and a five-eighths canopy would be recorded as having a girth of 31·25 in. By correlating these girth-canopy products with the average yield of the mature trees which had already given a straight girth-yield correlation coefficient of +0·357, a new coefficient was obtained indicated by the improved figure of +0·53.

(*d*) *Correlations between girths in 1935 and 1941 for seedlings and saplings.*—A final and minor question which has been investigated is whether the girth of a tree varies throughout its life in disproportion to its age and to an extent liable to throw out the relative order of trees in a given block over a number of years. That is, if certain trees in a block were of relatively great girth at two or three years of age, as a

result of experimental treatment during establishment, would that relative order still exist when the trees came into bearing and so influence the yields, provided of course that no differential factors interfered during the intervening years?

Some evidence was obtained on this question by measuring the girths of seven-year seedlings which had previously been measured when one year old. This indicated the extent of correlation between the girths of seedlings over a six-year gap and between the ages of one and seven years, the coefficient being positive and significant at 0·40.

The gap between similarly aged and older seedlings was bridged by measuring the girths of ten-year seedlings, which had also previously been examined when four years old. The correlation between these girths is also positive and significant, $r = 0{\cdot}73$. It is thus possible to assume that seedlings of large girth at two or three years old are likely to show the same relative superiority at ten or more years of age.

Summary

It is indicated that a positive correlation exists between stem-girth and canopy-area in young clove trees; between stem-girth and yield; and between stem-girth corrected for canopy and yield in older trees. As the girths of groups of young clove trees tend to remain in the same relative order of magnitude over a gap of several years, i.e. from the seedling to the bearing stage, it is held that stem-girth affords a useful criterion in field trials with young cloves in the pre-bearing stage.

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THE PRESENT AND POTENTIAL VALUE OF SUGAR-CANE BREEDING

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Introduction.—Although a few of the original sugar-cane varieties are still grown to some extent on a commercial scale, their cultivation is declining so fast that soon they will be of historic interest only. Their place is being taken by seedling varieties, produced at one or other of the breeding stations in cane-growing regions. When it is realized that sugar-cane was grown in India and China before the beginning of recorded history, and was introduced into the New World at the end of the fifteenth century, and that the first breeding work was not begun until 1888, the remarkable rate of the change-over to seedling canes can be appreciated. In little more than 50 years these varieties raised from seed have come to represent a very high proportion of the crop from which the world's cane sugar is manufactured.

Several factors have been responsible for the rapid decline of the old original varieties on which sugar-production had been based for so long. The spread of diseases as cultivation became more and more intensive, the growth of scientific knowledge, the desire for higher acre-yields brought about by the scramble for world sugar markets, and the tendency to extend cultivation into the sub-tropics, have all played their part. The success of the seedling varieties has been remarkable. Their wide-scale adoption in commercial cultivation is sufficient evidence of their superiority over the older canes, and the production of actual figures to prove the yield-increases they have brought about is hardly necessary to show how remunerative they have been.

In many instances the yield-increases due to the cultivation of new seedling varieties were spectacular. In Java, for instance, the increase in production of sugar per acre between 1885 and 1925 was over 300 per cent., and though not responsible for the entire increase, breeding is admitted to have been the main factor. Similar instances of the superiority of seedling canes when first they replaced the older varieties could be quoted for other countries. They were better adapted to their environment, whether owing to disease-resistance, to growth-type, or to that complex of physiological characters summed up as vigour. Once their commercial superiority had been clearly demonstrated the seedling canes enjoyed increasing popularity, and in a short time tens of thousands were being produced and tested annually at the breeding stations. The absorption of the best of these into commercial cultivation has resulted in most of the major sugar countries having improved varieties bred for and suited to their particular conditions. In addition certain seedling canes such as B.H. 10/12 and P.O.J. 2878, and more recently some of the Coimbatore series, occupy a prominent place in cultivation in countries other than those in which they were bred.

The Development of Sugar-cane Breeding

Sugar-cane breeding began in the same year in Java and Barbados, following the independent discovery of the fertility of sugar-cane flowers made in 1887–8 in the two countries. Naturally-occurring seedlings had been reported from various countries before this date, but experimental work on seedling-raising had not been attempted. Perromat began breeding work in Mauritius in 1891, and the breeding stations at Coimbatore (India) and Canal Point (Florida) started work in 1912 and 1918 respectively At the present time there are also breeding stations established in Hawaii, Queensland, Puerto Rico, Argentina, British Guiana, and elsewhere, as well as those in the countries mentioned above.

In the early days of sugar-cane breeding the work consisted chiefly of collecting the seed from wind-pollinated arrows, raising large populations of seedlings, and subjecting these to a scheme of testing and selection. As the sugar-cane is propagated vegetatively, the commercial varieties were—and still are—heterozygous for the majority of characters, so that random populations of seedlings showed a wide range of variation in most respects. Many valuable commercial varieties were produced by this method, which is dependent on chance, and it must be admitted that even at the present time in conjunction with a suitable selection technique the method is one by which an intelligent breeder may eventually produce valuable varieties. A genetical reason for this will be given later. Modern research work on sugar-cane breeding has aimed at reducing the empirical nature of the work, and there is no doubt that the foundations for future progress have been laid in a subject which bristles with difficulties.

Improvements in breeding methods date from the time when controlled crossing superseded the haphazard propagation of seedlings from chance-pollinated arrows. As early as 1912 Bovell had realized the importance of controlled crossing in Barbados, and had raised a series of seedlings from emasculated arrows pollinated by a known male variety. The famous cane B.H. 10/12 was produced from this series. On account of the dexterity required for the manipulation of the minute sugar-cane flowers, however, it was soon realized that the method was impracticable where large populations of seedlings were required, and the method was abandoned. Various mechanical devices for emasculating arrows, or for preventing anther dehiscence, have since been tried, but none has been found satisfactory.

The clue to the successful use of known 'male' and 'female' parents and thereby to the controlled breeding methods which are still in use was obtained in detailed examinations of the flowering phenomena in different varieties. Studies in Java, Hawaii, Barbados, Mauritius, and other countries showed that although many sugar-cane varieties are regularly hermaphrodite, in others total or partial sterility of the pollen grains occurs. Where this natural male sterility is complete, the variety can safely be used as a female parent without any possibility of selfed seedlings occurring in the progeny. Varieties which produce and shed

normal pollen, or which exhibit only partial pollen sterility, are used as male parents. Within the species *Saccharum officinarum*—the so-called 'noble' canes—male sterility is more rare than in the inter-specific hybrid varieties involving the blood of *S. spontaneum*, *S. barberi*, or *S. sinense*, where sterility frequently results from incompatibility of chromosomal complements. Consequently, and with a few notable exceptions, varieties of the noble canes are used as male parents in breeding work.

The adoption of the system outlined above, by which large seedling populations of known parentage can be raised, represents the first major advance in cane-breeding. The importance of pedigree is now generally recognized, and in the formulation of any constructive breeding scheme it is important that the parentage of every seedling should be beyond doubt. Unless this is the case, an element of hit-or-miss will have been introduced at the outset of the work. Where seedling populations are of known parentage the progeny test can be applied as a means of assessing the comparative values of parent varieties. Hence by an increasingly preponderant use of proven parent varieties the *average* quality of seedling populations will be raised from year to year, and the chances of obtaining valuable types by appropriate selection methods thereby progressively enhanced. The value of new parent varieties, which are introduced on an experimental scale into the breeding programme, can be rapidly ascertained by means of the progeny test.

In the production of improved sugar-cane varieties methods of selection and testing are second in importance only to the choice of parent varieties. In fact the meaning of the term 'sugar-cane breeding' is no longer restricted to the narrow sense of hybridization; it includes a study of the fundamental causes of variability in seedling populations, the differential responses shown by varieties under distinct environments, and the way in which adaptation to particular localities may be understood from a knowledge of individual growth-types.

Some Problems confronting the Sugar-cane Breeder

In the sugar-cane the quantitative characters are the most important economically. Tillering, growth-vigour, habit, thickness and weight of canes, drought-resistance, and juice-quality are some of the features on which varietal comparisons are based. Although it has been realized for some time that varieties used in breeding differ in prepotency with regard to certain of these qualities, it is only of late years that genetical studies on the inheritance of such quantitative characters have been considered important. Further, the commercial varieties are capable of indefinite vegetative propagation, so that the question of fixation of characters, and genetic purity of the stock, does not arise. Marked heterozygosity is therefore the natural outcome of the selection methods employed by the sugar-cane breeder, and his seedling populations show a wide range in form. In producing improved varieties there has up to now been little need of genetic analysis of the plant itself, for the extensive, if empirical, exploration of the naturally-occurring variability of seedling populations has sufficed. The improvements which have

been made in breeding and testing methods have been mainly due to the way in which the element of chance has been lessened.

The inheritance of yield in crop plants is concerned with the integration of a series of physiological processes, each of which must be determined before the fundamental genotypic analysis can be attempted. At present the results of work with various crop plants appear to indicate that yield, in common with the majority of quantitative characters, is polygenic. On the assumption that a large number of genes is operating, some of which are favourable to growth and some unfavourable, the wide and continuous yield-variation in populations from heterozygous stock can easily be understood. As the genes are located on the chromosomes the difficulty of combining all the favourable genes from two parent varieties in a single individual can be appreciated. And if it is permissible to assume that the number of genes associated with growth is greater than the number of chromosomes (40 pairs in noble canes), then certain chromosomes must carry two or more growth-genes, and the phenomenon of linkage adds a further complication.

Linkage damps the expression of variability in polygenic inheritance. Where unfavourable growth-genes are masked, owing to linkage with favourable ones, or incapable of detection owing to the mixed gene-constitution of the individual, their elimination by selection is evidently extremely difficult. In maize (which has only 10 pairs of chromosomes) recent work, mainly in the U.S.A., has increased greatly the knowledge of the genetic constitution of the plant. Of particular interest are the attempts which are now being made to locate favourable growth-genes. It is known that, for maize, only two generations of selfing are sufficient to fix the growth-genes, so that inbred lines are particularly favourable for genetical analysis in this plant. The method of linkage-testing, using marker genes in crosses between inbred lines, is one which promises to make possible the location of favourable growth-genes in certain cases; and one cannot foresee the advances which such research will yield within the next few years.

The question of dominance of genes associated with quantitative characters has grown in importance of late years, particularly in the study of heterosis. Here again much of the research has been carried out in the U.S.A. with inbred lines of maize and with selfed lines and interspecific crosses of the tomato.

In cultivated plants such evidence as is available would appear to suggest that, in the inheritance of polygenic characters, favourable genes frequently show at least partial dominance. The reason for this might be that continued selection over a number of years has tended to eliminate forms exhibiting dominance of unfavourable genes, thus upsetting the balance of dominance, positive and negative, which would be expected, *a priori*, to occur in unselected material. This concept of the dominance of favourable genes readily explains heterosis in F_1-populations from crosses between selfed lines. Also, provided a large number of gene pairs are involved, the reason why selfed lines as vigorous as F_1-crosses between inbred lines have not been obtained would be ascribed to linkage, with a consequent low probability that all the

favourable genes of two inbred parents would be combined in a single inbred line.

Heterosis, or hybrid vigour, has been put to valuable practical use in commercial maize-growing. It is no longer the mystery it was until recently, as a tentative explanation of its operation has been found. Physiologically it would appear that heterosis and dominance are merely degrees of identical phenomena. That this is so is indicated by the work of Powers (J. Agric. Res., 1941, **63**, 3) on crosses with *Lycopersicon*. In studying the mean period from seeding to first complete change of colour of fruits in two varieties of *Lycopersicon* and their F_1-hybrid Powers found that this feature showed complete dominance in 1938, and heterosis in 1939. Since the genotypes were constant for the two years it was clearly dependent on the environment as represented by the two years whether dominance or heterosis was manifested. Other work by the same investigator, including both intervarietal and interspecific crosses of *Lycopersicon*, in which environmental influence was controlled by a randomized-block layout, showed that whether dominance or heterosis was exhibited by the same feature was determined by the genotype alone.

In sugar-cane breeding heterosis results in the increased vigour frequently characteristic of hybrid seedling populations. It has been noted in Mauritius in crosses between the noble canes—*S. officinarum*—on the one hand, and both the Javan and Indian forms of *S. spontaneum* and also *S. robustum* on the other. It is but rarely that such first-generation hybrids are of immediate use commercially, because their juice-quality is generally unsatisfactory. As, however, they are propagated vegetatively, and the production of homozygous lines is unnecessary, they are of great value as parent varieties. The nobilization schemes in use at many sugar-cane breeding stations depend, in the first place, on the use of such vigorous first-generation hybrids in back-crosses with the noble canes.

Although comparatively little is known of the genetic constitution of the sugar-cane the actual chromosome numbers have been determined for most of the important varieties, and there is much information on the behaviour of chromosomes in interspecific crossing. The chromosome numbers of some hybrids in commercial cultivation are over 120, and it appears unlikely that any attempt to locate growth-genes in material of this degree of complexity could be attempted for the present.

The fact that the cultivated sugar-cane varieties are complex polyploid or aneuploid types introduces a further complication in studying polygenic inheritance. Also in inter-specific crosses chromosome behaviour is not always normal. For instance in a cross between a noble cane (80 chromosomes) and the Javan form of *S. spontaneum* (112 chromosomes) the chromosome number of the F_1 generation is not 96, the sum of the haploid numbers of the parents, as would be expected; it is 136, resulting from a doubling of the haploid noble chromosomes (2×40) plus the haploid number from the *spontaneum* parent (56). In the first back-cross of those hybrids to a noble cane a further doubling of the noble chromosomes occurs, and the offspring have 148

chromosomes. In subsequent back-crossing no further doubling occurs, but owing to irregularities in the reduction divisions and non-conjunction of chromosomes, the individuals are usually aneuploids with chromosome numbers only approximately equal to the sum of the haploid chromosome numbers of the parents.

From the foregoing example of chromosome behaviour in successive nobilizations of *S. spontaneum* it will be appreciated that the cytogenetical study of quantitative characters in sugar-cane is more complicated than in maize, with its 20 chromosomes. Many of the sugar-cane varieties now in commercial cultivation are bred from the third and fourth nobilization stages of *S. spontaneum*. Their vigour of growth in comparison with the noble canes is doubtless explained in part by the multiplication of favourable growth-genes due to the occurrence of polyploidy in their genealogy. However, it would be erroneous to suppose that the merits of a seedling should be in proportion to its chromosome number: other factors, such as sucrose-content of juice, disease-resistance, and a favourable balance of other hereditary features must also be considered. Seedlings with chromosome numbers as high as 170 have been produced by a suitable back-crossing technique (in this case by back-crossing hybrids to the *S. spontaneum* ancestor). Such forms are useless in cultivation on account of bad growth-habit and low juice-quality, though they do possess extreme vigour. Used as parents, however, they might produce seedling populations in which the chance of the occurrence of valuable individuals is enhanced. Any method which improves the genotypic average of first-year seedling populations is worthy of consideration.

It has been stated previously that much variation occurs in seedling populations, owing to the heterozygous nature of the parent stock. Also, assuming that numerous genes are responsible for the inheritance of quantitative characters, variation in these characters will be continuous and normal in distribution, and large populations will be necessary in order that as much of the range as possible shall be represented. Parenthetically it may be stated that if the *average* of a seedling population can be improved, then the chances of discovering valuable individuals in the extreme of the distribution-curve will be correspondingly greater. The methods by which the best seedlings can be identified in a population of this sort represent one of the most important aspects of sugar-cane breeding work. In order that selection methods shall be soundly based, a full understanding of the nature of variability in field populations is necessary.

Variation between individuals may be caused by differences in genotype or by differences in environment during development. The genotype of a seedling will remain constant on account of vegetative propagation (unless altered by subsequent mutation). It is decided by the genes contributed by the parents, is fixed at the original fertilization of the egg-cell, and is responsible for the trend of development under any environment. The extent of variation due to differences in environment during development is shown in any field planted with a single sugar-cane variety. Here the individual stools are of a single

clone, in which the genotype is fixed, though stool-to-stool variation on account of differences in soil fertility or sporadic distribution of pests and diseases may be considerable. Some figures for the variation found in an area of approximately ⅓ acre, planted in virgin canes of the variety R.P. 6, and carrying approximately 48 tons of cane per acre, have been given by Evans (Sug. Res. Stat., Mauritius, 1934, Bull. 3). In appearance the field was one of the most uniform on the estate, yet weights of individual stools varied from 0·7 to 51·2 kg., with a mean of 16·0 kg. and a coefficient of variability, 49·8. There is no doubt that environmental variation of this order profoundly influences the genotypic expression in seedling populations, and introduces an important source of error in selection work.

It will thus be evident that selection can be effective only when the differences upon which it is based are genotypic. The problem confronting the selector is to distinguish between genotypic and environmental variation under field conditions; where, as in first-year seedling populations, each individual is represented by a single stool, and several thousands are examined each year, the importance of a suitable selection technique cannot be over-estimated.

Where selections are made on a basis of weight over large areas then undue emphasis is laid on non-effective environmental variation, so that the weights of seedlings selected in this way need not be correlated with their yields in subsequent trials. Moreover, their *average* performance in second-year trials would clearly be poorer than that in the first-year trials from which they were selected. Data proving this have been published by Hill (Sug. Res. Stat., Mauritius, 1935, Bull. 8) and a consideration of the principles involved was given by McIntosh (B.W.I. Cent. Sug.-cane Br. Stat., Barbados, 1935, Bull. 9) and by Stevenson, (Sug. Res. Stat., Dept. Agric., Mauritius, 1938, 9th Ann. Rept.).

The effect of environmental variation, which in later trials can be largely eliminated by plot-replication and statistical analysis, must be accepted as a necessary evil in first-year seedling trials. If, however, its presence as a possible modifier of genotypic expression is recognized, certain precautions can be taken to lessen its influence. Land which is known to be irregular in fertility will be avoided, as far as possible. Secondly, at the time of selection, more importance will be attached to relative weights of individuals within comparatively small areas than to actual recorded weights of the whole population. As the best seedlings must occur at random in the field, selections from such small areas will include a high proportion of them. Unless these principles are made the basis of first-year selection the weight per stool will be found an unreliable and disappointing criterion.

Trend of Present-day Research in Sugar-cane Breeding

The rapid progress made in the early stages of sugar-cane breeding on modern lines has already been referred to. Selective advance is a continual process, but becomes increasingly difficult as a succession of improved varieties comes into cultivation. The law of diminishing returns can be discerned in the results of breeding work at the present

time, and it appears that a limit to progress might soon be reached unless efforts to reduce the empirical aspect of the work are successful. The necessity for some empiricism in the present breeding methods has already been explained. This empiricism can be finally eliminated only by means of long-range research on fundamentals—research which might appear to have no immediate practical application, and which would inevitably be opposed by the continuous demand for results if carried out in any institution whose purpose is in any way practical. Results in sugar-cane breeding will be judged by previous accomplishments in variety improvement: they will be represented by a series of varieties to which planters can point with pride, and from which they derive obvious benefit.

The foregoing premise leads to a consideration of the trend of modern cane-breeding developments, and how varietal improvement can be effected in the immediate future.

Research work in cane-breeding can be resolved into two main lines: evaluation of the potentialities of parent varieties, and the technique of selection applied to seedling progenies: all investigations are directly or indirectly related to one or other of these. The progeny test has already been referred to. It is the most useful practical means of assessing the value of parent varieties, and also lends itself to a direct study of inheritance of many qualities in breeding. McIntosh and Stevenson (B.W.I. Cent. Sug.-cane Br. Stat., Barbados, 1935, Bull. 8) and Stevenson (Sug. Res. Stat., Mauritius, 1939, Bull. 15) have shown its use in breeding for resistance to gumming disease. Where immediate practical application is desirable in the geneticist's work, progeny-testing proves the most satisfactory method of studying the inheritance of such features as juice-quality, male-sterility, and resistance to low temperatures. There is a large field still to be explored in breeding for resistance to certain diseases (e.g. chlorotic streak), and to most sugar-cane pests (borer, frog-hopper, *Phytalus* grubs, &c.) in which the active co-operation of plant pathologists and entomologists respectively is the first essential. In such cases it is evident that unless direct field methods for determining the susceptibility of varieties can be worked out, geneticists cannot base their inheritance studies on a sound foundation. The problem is admittedly a difficult one. Resistance to borer, for instance, would appear to depend not only on an innate quality of canes making them repellant to the insect, but also on resistance to secondary rotting organisms, vigour of growth leading to rapid recovery from injury, and other factors.

Where resistance and susceptibility to a definite disease are clearly defined and can be easily demonstrated under field conditions, breeding work has resulted in the production of resistant varieties so long as a range in susceptibility of parent varieties has existed. The menace of the deseases sereh, mosaic streak, and gumming has been removed by the work of geneticists, who can now incorporate resistance to these diseases with other desirable qualities in their seedlings.

In the diseases mosaic and sereh it appears that the genes responsible for immunity are carried by the chromosomes of *S. spontaneum*. Kassoer, a natural hybrid of this wild species, is immune. In successive nobiliza-

tions of the Kassoer blood-line, P.O.J. 2364, with 28 *spontaneum* chromosomes, is immune; P.O.J. 2878, with about 14 *spontaneum* chromosomes, is not immune but has sufficient resistance for commercial purposes; seedlings of the fourth nobilization are more susceptible to mosaic and sereh, though some variation between individuals occurs in this respect. These seedlings have about seven *spontaneum* chromosomes, but on account of irregularities in the reduction-division and non-conjunction of chromosomes, the exact number of *spontaneum* chromosomes is uncertain. These facts indicate that in this case disease-resistance behaves as a polygenic character and is correlated with the number of *spontaneum* chromosomes present.

The P.O.J. nobilization series is quoted because it is the best known. Similar series exist in other countries, and are yielding valuable new varieties characterized by resistance to various diseases. In Mauritius the Uba Marot blood-line is a nobilization of the 64-chromosome Indian *S. spontaneum* (cf. Stevenson, Sug. Res. Stat., Mauritius, 1940, Bull. 17). With individuals in this series resistance-testing shows that immunity to gumming disease is also associated with the *spontaneum* chromosomes, though the situation is complicated by the fact that in the noble canes themselves a degree of resistance almost amounting to immunity is sometimes found.

The value of cyto-genetical studies in connexion with disease-resistance, directing lines of research which could previously be followed up by trial and error alone, has been clearly demonstrated. Work in progress at present, including interspecific crosses with the *S. robustum* forms from New Guinea and the cold-resistant *S. spontaneum*, recently obtained in Turkestan by the Brandes expedition to central Asia, will undoubtedly yield varieties incorporating valuable qualities for use in breeding, and might conceivably result in making possible the commercial cultivation of sugar-cane under conditions and in latitudes where it has hitherto been impracticable.

Research has also shown the inter-relationships between the different *Saccharum* species, and the different forms sometimes met with in a single species. It has given an explanation of the poor fertility of many interspecific crosses due to incompatibility of chromosomal complements—an incompatibility which might eventually be overcome by the use of artificially induced polyploidy, using the colchicine technique. By the use of this drug in appropriate concentrations polyploids can be easily induced in many plants, and forms of increased size and vigour obtained. In the sugar-cane, although various modifications can be produced in treated seedling populations, the writer is not aware of any well-authenticated case in which an improved variety has been obtained. The fact that the existing sugar-cane varieties are, in the first place, complex polyploids may account for this: also the degree of variation normally met with in seedling populations makes difficult the definite recognition of artificially induced modifications. Nevertheless information on the action of colchicine and similar drugs in sugar-cane breeding is becoming available, and there is hope that the technique may eventually prove useful.

As a result of the improved seedling varieties coming into cultivation in increasing numbers the era of the old general-purpose variety is ending. A new variety is frequently found to give its best performance under a particular set of environmental conditions: there is every indication that in any sugar-cane-growing country the ultimate solution of the question of maximum production will be found in a number of varieties, each bred for, and particularly adapted to, a rather narrow environmental range. Differential responses between varieties under various conditions are frequently very marked, and the importance of testing each promising new variety in several different environments is generally recognized. In first-year trials the necessity for testing each seedling under one set of conditions only, introduces a major limitation to the reliability of the work, no matter how carefully the selections are made. If this fact is constantly borne in mind then the source of error will be reduced to its least proportions, for there are certain indications in the growth-characteristics of seedlings in any environment which give a clue to the conditions to which they might be best suited. In searching for the reasons underlying the differential responses exhibited by varieties in various localities McIntosh (Agric. J., Barbados, 1934, **3** No. 1) first recognized the importance of growth and periodicity studies in distinguishing particular varietal growth types. From a study of such features as the time and extent of tiller-formation, cane growth-rate, and arrowing it is now possible to forecast with fair accuracy the type of conditions to which a seedling will be best suited. As a result of work now in progress it is likely that it will soon be possible to select seedlings most promising for trial under infertile soil conditions, or where damage by root-eating insects is serious, from a knowledge of seedling growth-types.

The rapid succession of new varieties now being produced necessarily shortens their period of commercial popularity. The superiority of a new variety is in itself sufficient to ensure the eclipse of its predecessor; there seems to be no limit to the process so long as variety-improvement, no matter how small, continues. The question whether the modern varieties are deficient in stamina has been raised (Int. Sugar J., 1941, **43**, 511) in commenting on a paper by the writer: 'It is arguable that except where resistance to disease is specifically aimed at, the tendency in breeding is to concentrate on the characters of major economic importance to the neglect of those more subtle characters rather vaguely summed up by the term stamina. There is something more than a suspicion, though possibly falling short of definite proof, that many of the products of the plant-breeder are deficient in these characters.'

This view is a specious one. It is true in so far as stamina is understood literally to refer to the power to endure in cultivation for a long time. If, however, the popularity of a variety declines simply on account of the availability of higher-yielding ones, then it would be a mistake to seek a reason in lack of stamina. The conviction that the old is necessarily better in certain ways than the new is rather typical of the conservatism of planting communities everywhere. The writer has on many occasions heard the view expressed by planters of the older

generation, with years of practical experience behind them, that the new sugar-cane varieties 'do not look as though they will last'. Why this should be so is not known, and for this reason the view is almost impossible to refute. Equally deep-rooted is the impression that, through some mysterious agency, varieties will deteriorate when propagated asexually over long periods. There is no scientific foundation for this belief: such deterioration as has undoubtedly occurred in some cases can always be ascribed to a definite cause, frequently to a disease newly introduced or of increasing virulence, to which the variety is susceptible.

Parent varieties available to the sugar-cane geneticist involve varying proportions of the blood of no fewer than five *Saccharum* species. Reaction to specific diseases varies greatly in this material: some of the new commercial varieties show a satisfactory resistance to one or more diseases, but it is rare to find a variety combining resistance to all the important diseases of the country in which it is grown with other desirable qualities. For this reason co-operative work between plant pathologists and geneticists, aiming at the production of superior disease-resistant varieties, will continue to play an important part in the breeding work of the future.

For reasons already given it appears unlikely that the big advances seen in variety-improvement will be repeated. Also, the limiting factors set by cultural methods and rainfall-distribution are increasingly felt as agriculture becomes more and more intensive. There is one direction, however, in which large advances can confidently be expected. This is in breeding better-quality varieties for growth in areas where fundamental infertility of soil, or the presence of some serious disease (e.g. mosaic) or pest (e.g. frog-hopper), has rendered the cultivation of the high-grade thick-cane varieties unprofitable. Work now in progress is already yielding improved varieties for such particular localities.

Sugar-cane breeding is a slow process, since a comprehensive testing scheme is necessary, and it is generally from five to seven years after its breeding that a new variety is introduced into commercial cultivation. The best of the varieties available at present have certain defects, and the ideal variety is but vaguely formulated, for changing conditions or the incidence of a new disease or pest may at any time call for resistant varieties of good quality at short notice. Plasticity is essential, as in all biological investigations, no matter how much routine work is also involved: and each advance, trivial though it may seem in relation to the ultimate objective, is a reward and an encouragement in itself.

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THE ROTHAMSTED EXPERIMENTS ON MANGOLDS 1872–1940

PART I. EFFECT OF MANURES ON YIELD OF ROOTS

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MANGOLDS had not long been commonly grown in England at the time when Lawes began experimenting about 1835. They did not come to us from France or the Low Countries, the regions from which in the seventeenth and eighteenth centuries we had received turnips, clover, lucerne, sainfoin, and other valuable crops; instead they came from Germany with which at that time we had but little agricultural connexion. The first consignment of seed appears to have been sent in 1786 by T. Boothby Parkins of Metz to Sir Richard Jebb, who gave some to the Royal Society of Arts for distribution. Shortly afterwards followed two translations of the Abbé de Commerell's pamphlet[1] describing the German method of growth and the storage of the roots in clamps. Experience with these early batches of seeds is recorded by various growers in the *Annals of Agriculture*:[2] both leaves and roots were used, the leaves being hand-plucked when they bent over towards the ground. Little further progress was made during the French Revolution and the Napoleonic wars; mangolds are not mentioned in the great surveys made at the end of the eighteenth and in the first decade of the nineteenth century,[3] and it is not till 1815 that accounts of mangold-growing on the farm scale appear.[4] From that time onwards, however, an increasing number of farmers grew the crop. These early accounts lay stress on the high yields—50 tons per acre is an example given by Gibson[5]—the power to withstand drought, and the freedom from the insects which periodically ravaged the turnip crop, so that, as Gibson said, the mangold crop 'stands unrivalled for its utility at a period of scarcity in April, May, and even June'. The Abbé de Commerell had indeed called it 'la racine de disette'—scarcity root—this being the translation of what he thought was the German name 'Mangel wurzel'. But, as Lettson pointed out in his preface to the Abbé's pamphlet, the Abbé had mis-

[1] T. Boothby Parkins, *Trans. Soc. Encouragement of Arts*, 1787, **5**, 52. Abbé de Commerell, *An Account of the Culture and Use of the Mangel Wurzel or Root of Scarcity*, translated from the French by J. C. Lettson, 2nd and 3rd editions, 1787. *A Treatise on the Culture, Use and Advantages of the Plant called Scarcity-root*, translated by M. Sibille, 1787.

[2] Earl of Oxford, *Ann. Agric.*, 1789, **12**, 49; William Pitt, ibid., 51: T. Wilson, ibid., 380.

[3] There is no mention of them in Marshall's tours (1787 to 1798) or in Young's *Agriculture of Suffolk* (1804) or Kent's *Agriculture of Norfolk* (1813).

[4] Mr. J. Gunston of Park Farm, Holkham, informs me that Coke in his manuscript 'Book of Observations' records the weight of roots and leaves of a mangold crop grown on the grounds of Mr. W. Wulrot in 1831. A square pole gave results equivalent to 64·4 tons of roots and 9·5 tons of leaves per acre, which although possible is very exceptional.

[5] F. Gibson, *Farmers' Magazine*, Edinburgh, 1815, **16**, 70.

heard the German name, which is Mangold,[1] and has nothing to do with 'scarcity'. Unfortunately the Abbé's error still persists and many writers quite erroneously use the name 'mangel'. Coke of Norfolk grew mangolds on his farm at Holkham, and Dr. Rigby in 1817 records seeing there 'a crop in a good state.'[2] Earl Spencer[3] made feeding trials in 1825 and 1826, which are interesting as early examples of technique. But mangolds were not yet widely grown, and in Lawes's first account of them in 1847 he recommends their more general use in the south of England and wherever low rainfall makes turnip culture uncertain, adding too that they are 'capable of producing a larger amount of solid food per acre than any other crop in a rotation'.[4] He did not, however, start field experiments till 1876, and by that time the crop was widely grown, the area exceeding 350,000 acres in England and Wales; the chief counties were, in order of acreage: Norfolk, Suffolk, Essex, Devon, Lincolnshire, Cambridgeshire. Farmers' experience on the manuring of the crop had been summarized by Caird[5] showing that salt was particularly beneficial whereas phosphate gave but little return, this being in sharp contradistinction to turnips. Definite field experiments were made by Augustus Voelcker,[6] who showed the advantage of nitrate of soda and of potash, especially a mixture like that afterwards called potash salts. By 1875 Morton's *Cyclopedia of Agriculture* was able to give a full and very good account of the culture and manuring of the crop.

Lawes and Gilbert therefore began the experiment with a foundation of well-ascertained fact, especially so far as the mineral fertilizers were concerned. They considered, however, that there was still room for further work on the source of nitrogen for the crop, a problem in which they never lost their interest. Root crops had been regarded by agriculturists as restorers of fertility, and it had been assumed that their large leaves enabled them to absorb ammonia from the air and to continue their growth independently of added nitrogenous fertilizer. If the plants were given a start with a small dressing of nitrogen, they might be expected to continue growth on what they picked up from the atmosphere. Lawes and Gilbert had shown that this assumption was quite groundless in the case of turnips and sugar-beet: the growth of the crop was determined by the amount of nitrogen supplied in the fertilizer so long as the proper mineral substances were present. They now proceeded to see if mangolds also behaved like the other two root crops.

The Barnfield Experiment

Barnfield adjoins Agdell field and lies about a quarter of a mile from Broadbalk: its soil, however, is not dissimilar. It had been under

[1] In the oldest book on German agriculture in the Rothamsted Library (*Georgica Curiosa Aucta*, &c., Herr von Hohberg, Nuremburg, 1687) 'roots' (*Rüben*) are included among the winter cattle-foods, but the name 'mangold' is used only for the beet grown as a vegetable for human food.

[2] Edward Rigby, *Holkham, Its Agriculture*, &c. 1817.

[3] Earl Spencer, *Farmers' Journal* 1826: repeated in *J. Roy. Agric. Soc.*, 1841, **2**, 296.

[4] J. B. Lawes, *J. Roy. Agric. Soc.*, 1847, **8**, 563.

[5] Jas. Caird, *J. Roy. Agric. Soc.*, 1856, **17**, 400.

[6] Augustus Voelcker, *J. Roy. Agric. Soc.*, 1864, **25**, 240; 1867, ii, **3**, 86; 1870, ii, **6**, 155; 1871, ii, **7**, 382, and other papers.

experiment since 1843; for most of the time swedes were grown, but they were replaced by sugar-beet for the period 1871–5. The scheme of manuring for the mangolds followed that for sugar-beet, which in turn had closely followed that for swedes: there had been practically no change since 1861 and many of the plots had received the same

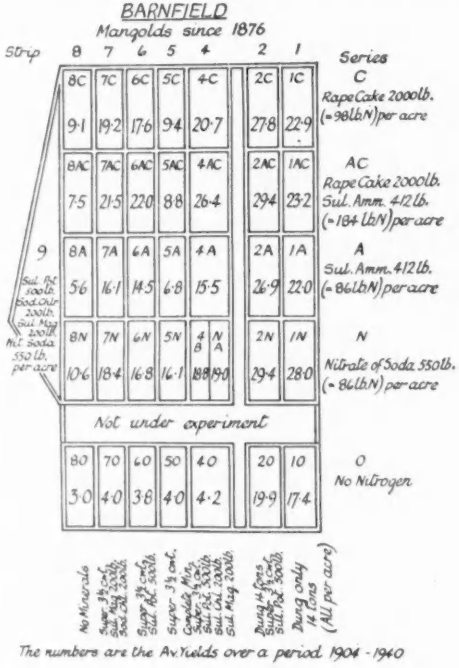

BARNFIELD
Mangolds since 1876
Strip 8 7 6 5 4 2 1 Series
8C 7C 6C 5C 4C 2C 1C C
Rape Cake 2000lb.
(=98lb.N) per acre
9·1 19·2 17·6 9·4 20·7 27·8 22·9
8AC 7AC 6AC 5AC 4AC 2AC 1AC AC
Rape Cake 2000lb.
Sul. Amm. 412lb.
(=184 lb.N) per acre
7·5 21·5 22·0 8·8 26·4 29·4 23·2
9 8A 7A 6A 5A 4A 2A 1A A
Sul. Amm. 412lb.
(=86lb.N) per acre
5·6 16·1 14·5 6·8 15·5 26·9 22·0
8N 7N 6N 5N 4B 4A 2N 1N N
Nitrate of Soda 350lb.
(=86lb.N) per acre
10·6 18·4 16·8 16·1 8·8 19·0 29·4 28·0
Not under experiment
8O 7O 6O 5O 4O 2O 1O O
No Nitrogen
3·0 4·0 3·8 4·0 4·2 19·9 17·4
No Minerals
Super 3½ cwt.
Sul. Pot. 500lb.
Sul. Mag 200lb.
Super 3½ cwt.
Sul. Pot. 500lb.
Super 3½ cwt.
Complete Mix.
Super 3½ cwt.
Sul. Pot. 500lb.
Sul. Mag 200lb.
Dung 14 tons
Super 3½ cwt.
Sul. Pot. 500lb.
Dung only
14 tons
(All per acre)
The numbers are the Av. Yields over a period 1904 - 1940

FIG. 1

manures, though not always in the same quantities, since 1845. Fig. 1 shows the plan of experiment as it has been since 1902, when a few minor changes were made.

The field is divided into 8 strips running north and south along its greatest length; these receive respectively (1) (west end) farmyard manure, 14 tons per acre; (2) farmyard manure as on strip 1, 3½ cwt. superphosphate, 500 lb. sulphate of potash;[1] (3) unmanured;[2] (4) 3½ cwt. superphosphate, 500 lb. sulphate of potash, 200 lb. sulphate of magnesia, and 200 lb. sodium chloride; (5) superphosphate as on strip 4; (6) P and K as on strip 4; (7) P, Mg, Na as on strip 4;[3] (8) no manure. The mineral manures are given just before seeding.

[1] Since 1895; prior to that farmyard manure + 3½ cwt. superphosphate only.

[2] Strip 3 was very narrow and was discarded in 1902 and left as a buffer strip between those with and those without farmyard manure.

[3] Since 1903 only; prior to that P and K as on strip 4 + 36½ lb. ammonium salts.

These strips are divided crosswise into five for nitrogenous dressings, these being: (1) none (north end); (2) nitrate of soda (86 lb. N per acre); (3) sulphate of ammonia[1] (86 lb. N per acre); (4) rape cake (2,000 lb.) and sulphate of ammonia (98+86 = 184 lb. N per acre); (5) rape cake (98 lb. N per acre). The sulphate of ammonia and nitrate of soda were given with the minerals till 1896, then as top-dressing when the plants were well up, till 1917, but from 1918 onwards one-third has been given with the minerals and two-thirds as top-dressing.

There are thus 35 plots in this main series, and these have remained unchanged in treatment since 1861, excepting only strips 2 and 7 which were altered in 1895 and 1902 respectively. The plots are mostly about $\frac{1}{7}$ acre and the area under experiment is about 8 acres.

Roots and leaves are weighed, the roots are carted off, and the leaves spread on the ground and ploughed in.

The seed was sown on ridges till 1929, since when it has been sown on the flat. It was formerly dibbled in,[2] but since 1896 it has been drilled 26 in. between the rows and the plants singled to about 15 in. The number of plants per acre is about 16,000.

Thus there were two periods during which the treatments continued unchanged, from 1876 to 1894 and from 1904 to 1940. The mean yields of roots on each plot for these two periods are given in Table 1.

TABLE 1. *Mangolds, Barnfield: Mean Yield of Roots; Tons per Acre**

(*a*) 18 years, 1876–94. (*b*) 32 years, 1904–40†

Plot		*No Nitrogen O*		*Sulphate of ammonia A*		*Nitrate of soda N*		*Rape cake C*		*Rape cake+ Sulphate of ammonia AC*	
		1876–94	*1904–40*	*1876–94*	*1904–40*	*1876–94*	*1904–40*	*1876–94*	*1904–40*	*1876–94*	*1904–40*
8	No P or K	3·78	2·99	6·02	5·60	10·25	10·55	10·19	8·28	10·08	7·46
5	P	5·02	4·01	8·30	6·80	15·70	16·06	11·96	9·45	11·16	8·84
6	P K	4·46	3·76	13·69	14·51	15·52	16·83	18·01	17·55	22·14	22·00
7	P Na Mg‡	(5·87)	3·95	(15·04)	16·14	(15·92)	18·45	(18·87)	19·19	(21·95)	21·50
4	P K Na Mg	5·34	4·21	15·51	15·52	18·30	18·98	20·67	20·67	25·02	26·45
1	FYM	16·77	17·38	22·11	21·95	23·21	27·99	23·63	22·98	24·50	23·20
2	FYM, PK‡	(17·01)	19·93	(21·36)	26·88	(24·23)	29·36	(23·29)	27·75	(23·46)	29·45

* The average yield of mangolds in Great Britain for the ten years 1928–37 was 18·5 tons per acre.
† The crop failed in 1908, 1927, 1930, 1931, 1935.
‡ The figures in brackets are means for the early period when the treatment differed from that given later. See p. 51.

The main conclusions were given by Lawes and Gilbert in their 1895 summary[3] and discussed in detail in 1906[4] by A. D. Hall, who set them out in diagram form (Fig. 2).

Nitrogenous fertilizers gave results similar to those obtained with

[1] Prior to 1917, however, this plot received 'ammonium salts' consisting of a mixture of equal weights of sulphate of ammonia and muriate of ammonia, except in 1887, when it had sulphate of ammonia only.

[2] Except 1882, 1884, and 1885, when it was drilled.

[3] *Agricultural Investigations at Rothamsted during a Period of 50 Years*, U.S. Dept. Agric. 1895, Bull. No. 22, and *Trans. High. Agric. Soc.* 1895, Ser. 5, **7**, 11–354.

[4] A. D. Hall, *J. Roy. Agric. Soc.* 1902, **63**, 27–59.

turnips and sugar-beet. In absence of added nitrogen the yields were all low, only about 5 tons per acre. A small dressing of sulphate of ammonia (7·8 lb. nitrogen per acre) was almost ineffective, adding only 1·4 tons per acre; showing that the plants could not get along with the small nitrogenous starter. Larger nitrogenous dressings gave greater

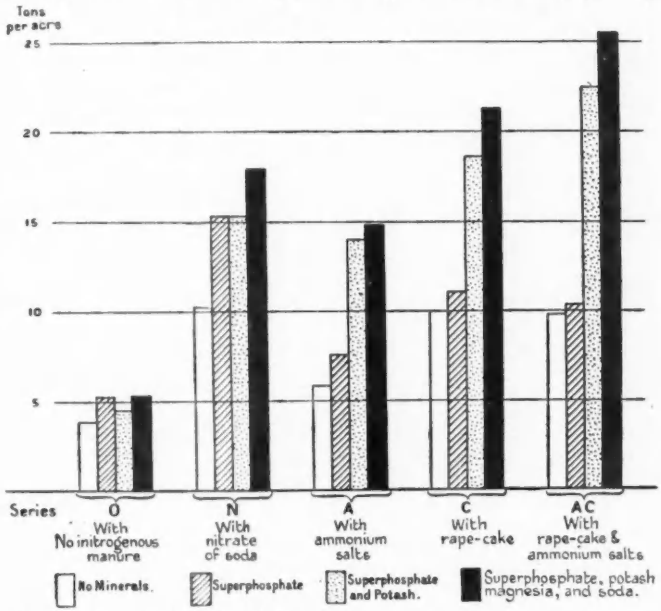


FIG. 2. *Mangel Wurzel.* Effect of various mineral manures. Average produce of roots per acre, 1876–1902

returns, but the fertilizers differed among themselves in effectiveness more than for swedes, though no more than for sugar-beet.[1] Nitrate of soda and rape cake were more effective than sulphate of ammonia.

The mineral manures, on the other hand, gave very different results with swedes and with mangolds. With swedes, superphosphate had increased the yield given by sulphate of ammonia to its maximum, and nothing was gained by adding sulphate of potash. With mangolds, however, the superphosphate increased the effect of sulphate of ammonia only by about 1½–2½ tons per acre, but potash gave a further 4 or 5 tons, and addition of salt and sulphate of magnesia still further raised the yield. These effects of potash and of salt were among the most striking of the older Rothamsted experiments.

Experiments with Inorganic Fertilizers

Comparison of nitrate of soda and sulphate of ammonia.—The responses to these two fertilizers in different conditions are set out in Table 2.

[1] The sugar-beet of those days, however, was very different from ours of to-day.

TABLE 2. *Increase of Yield of Roots produced by Nitrogenous Fertilizers (86 lb. N per acre); Tons per Acre*

	No minerals	P	PK	P Na Mg	PK Na Mg
Sulphate of ammonia					
1876–94 . . .	2·24	3·28	9·23	..	10·17
1904–40 . . .	2·61	2·79	10·75	12·19	11·31
Nitrate of soda					
1876–94 . . .	6·47	10·68	11·06	..	12·96
1904–40 . . .	7·56	12·05	13·07	14·50	14·77

The response to sulphate of ammonia is but little affected by superphosphate, but is much increased by potash, soda, and magnesia.

The response to nitrate of soda, on the other hand, is greatly increased by superphosphate, but not much further increased by potash, soda, and magnesia.

Nitrate of soda is much more effective than sulphate of ammonia in absence of P, K, and Na, but not when they are supplied. Indeed, a mixture of sulphate of ammonia and salt is as effective as nitrate of soda. The superiority of the nitrate of soda is therefore due not to its nitrate but to its sodium, and with adequate sodium or potassium supply the ammoniacal nitrogen is as effective as nitrate. This comes out more clearly from Table 3, where the actual yields are given instead of the responses.

TABLE 3. *Comparison of Sulphate of Ammonia+Salt with Nitrate of Soda in presence of Superphosphate: Mean Yield of Roots; Tons per Acre*

	Sulphate of ammonia		*Nitrate of soda*	*Superiority of nitrate of soda over sulphate of ammonia and salt*
	No Na *or* Mg	*+salt and magnesia*	*No* Na *or* Mg	
No potash				
1904–40 . .	6·80	16·14	16·06	Nil
Potash given				
1876–94 . .	13·67	15·51	15·52	Nil
1904–40 . .	14·51	15·52	16·83	1·3

Superphosphate.—The experiment as originally designed shows the effect of superphosphate in absence of potash only. This is very different for the different nitrogenous fertilizers; the increases given by superphosphate have been, in tons per acre:

Plots	*No nitrogen 5O–8O*	*Sulphate of ammonia 5A–8A*	*Nitrate of soda 5N–8N*	*Rape cake 5C–8C*	*Rape cake and sulphate of ammonia 5AC–8AC*
1876–94	1·24	2·28	5·45	1·77	1·08
1904–40	1·02	1·20	5·51	1·17	1·38

In presence of sulphate of ammonia the superphosphate gave during the first period an increase of 2·3 tons per acre which in the second period became reduced to 1·2 tons because of a fall in yield of plot 5A. The increase produced in presence of rape cake was even smaller. In absence of potash and soda the superphosphate is, therefore, relatively ineffective.

Entirely different results were obtained, however, in presence of sodium nitrate. This considerably increased the effectiveness of the superphosphate; moreover, the effectiveness was maintained; the superphosphate added 5·45 tons per acre per annum as the average of the first 18 years and 5·51 tons as the average of the last 32 years. This suggests that superphosphate is more effective when given in the presence of soda.

In its original form the experiment gave no information about the behaviour of superphosphate in presence of potash. An attempt was made to rectify this in 1903, and plot 9, which had until then received dung, phosphate, and sulphate of ammonia, had its treatment changed to nitrate of soda and the full minerals of plot 4 (Na, Mg, K) but without superphosphate, in the hope that the difference in yield between plots 4NA and 9 would ultimately give the effect of superphosphate in the presence of potash and soda. Changes of this kind are never satisfactory. The wide difference in previous treatment of the two plots makes comparison impossible, at least for an indefinite period. For the first 20 years after the change, plot 9 yielded better than 4NA (Table 4), presumably the result of the 27 annual dressings of farmyard manure which it had received; then it fell below 4N, which may be attributed to the lack of phosphate: in the last 5 years the difference has averaged 1·8 tons per acre. This is very much less than the average increase of 6·1 tons produced in the same period by superphosphate in the absence of potash and soda.

TABLE 4. *Comparison of the Mean Yield of Roots of Plot 4 NA and Plot 9, Barnfield; Tons per Acre*

Plot	*Treatment*	*1893–1902*	*1903–7 (5 years)*	*1916–21 (6 years)*	*1922–35 (10 years)*	*1936–40 (5 years)*
4NA	NPKNaMg	15·64	17·22	21·03	19·62	19·49
9	NKNaMg	17·75	26·27	22·74	19·14	17·67

The area harvested of plot 9 was not recorded in the period 1908–15.

1936–40	Apparent increase produced by superphosphate in presence of potash and soda	1·82
	Increase produced by superphosphate in absence of potash and soda (Plots 5N–8N)	6·06

Potassium, sodium, and magnesium salts.—The effects of potassium and sodium salts on the mangold crop are so similar that they can be discussed together. Unfortunately, magnesium was always given with the sodium so that the effects of these two elements cannot be separated. Later experiments, however, indicate that the main if not the entire

action of the mixture is due to the sodium salt. The crop responses are shown in Table 5.

TABLE 5. *Increased Yield of Roots, Tons per Acre, produced by Potash and Soda and Magnesia, in Presence of Phosphate*

		N *supplied, lb. per acre*				
			86		*98*	*184*
		None	*Nitrate of soda*	*Sulphate of ammonia*	*Rape cake*	*Sulphate of ammonia and rape cake*
K	1876–94	−0·56	−0·18	5·39	6·05	10·98
	1904–40	−0·25	0·77	7·71	8·10	13·16
Na+Mg	1904–40	−0·06	2·39	9·34	10·91	12·66
K, Na+Mg	1876–94	0·32	2·60	7·21	8·71	13·86
	1904–40	0·20	2·92	8·72	11·22	17·61
Gain by adding:						
K to Na and Mg (1904–40)		0·26	0·53	−0·62	0·31	4·95
Na and Mg to K		0·45	2·15	1·01	3·12	4·45

Potassium and sodium and magnesium had little effect in absence of nitrogen; they depressed the yield slightly, except when given together.

In presence of nitrogen the effects depend on its source and amount. With nitrate of soda they are only small: with sulphate of ammonia and with rape cake they are much greater, and they increase as the supply of nitrogen increases. Further, the effects are more pronounced in the later than in the earlier period.

The mixture of sodium and magnesium salts was more effective than the potassium salt, although the quantity of sodium which it supplies is less than the chemical equivalent of the potassium.[1] Nothing is gained by adding potassium to sodium and magnesium except when large quantities of nitrogen are given, and apparently salt can quite well replace potash as a fertilizer for mangolds.

Later experiments show that sodium chloride without magnesium sulphate notably increases the yield of mangolds, but there is no evidence that either sodium or chloride is essential to the growth of the plant. The subject is more suitable for pot-culture than for field experiment, but two indications are furnished from Barnfield:

Since 1904 plot 4N, receiving nitrate of soda and complete minerals, has been divided into two parts, one continuing to receive the old treatment while the other still received potash, but the sodium salts were replaced by calcium chloride and nitrate. This has had no effect on the yield:

	Sodium salts	*Calcium salts No sodium*
Plot	*4NA*	*4NB*
Mean yield, tons per acre, 32 years, 1904–40 . .	18·98	18·78

[1] The potassium sulphate supplies 250 lb. K_2O, and the sodium chloride 100 lb. Na_2O; 150 lb. K_2O is chemically equivalent to 100 lb. Na_2O.

In so far as any conclusion is permissible from a single-plot experiment, the result indicates that sodium is not essential, at least in the presence of potassium, but can be fully replaced by calcium.

No direct test has been made of the action of chloride, but some indirect information is available. Up to 1902 the 'ammonium salts' used on series A and AC consisted of a mixture of equal weights of muriate and sulphate of ammonia, but after 1902 sulphate only was given. There is, however, no sign of any falling off in yield in the second period so long as potash is supplied, though there is a fall where this is withheld, which can be fully explained as due to lack of potash:

	Mean yield, tons per acre		
	PK	P, *no* K	*No* P *or* K
Plot	*6A*	*5A*	*8A*
Chloride given (1876–94)	13·69	8·30	6·02
No chloride (1904–40)	14·51	6·80	5·60

Crowther and Yates[1] found from their survey of a large number of experiments in Great Britain on mangolds grown in rotation that the average response to a standard dressing of potash (0·5 cwt. K_2O per acre) in the absence of dung was 1·9 tons of roots per acre. The responses to potash on Barnfield, in the period 1904–40, calculated for the same dressing by means of the standard response-curve given by Crowther and Yates are, in tons per acre:

In presence of:	*No* N	*Nitrate of soda*	*Sulphate of ammonia*	*Rape cake*	*Rape cake and sulphate of ammonia*
	−0·15	0·47	4·73	4·97	8·07

Except in the absence of nitrogen or in the presence of nitrate of soda, the effects on Barnfield are all much larger than in the rotation experiments, presumably because of the exhaustion of potash on the plots from which it has been withheld for a long period.

Crowther and Yates also found that in the rotation experiments the average response to a dressing of 4 cwt. salt per acre, in the absence of farmyard manure, was, in tons of roots per acre:

In presence of:	*No* K	K
	3·4	2·7

Comparison with the figures given in Table 4 shows that on Barnfield the mixture of salt and sulphate of magnesia gave much greater average increases, except in the absence of nitrogen, and in the presence of nitrate of soda, although the quantity of salt applied was only 200 lb. per acre; the interaction between salt and potash also was more pronounced.

[1] *Empire J. Expt. Agric.*, 1941, **9**, 77–97.

Experiments with Organic Manures

Farmyard manure.—Used alone at the rate of 14 tons per acre (about 200 lb. N), farmyard manure has given an average yield of 17 tons mangolds per acre, which is somewhat below that given by nitrate of soda and complete minerals. This has been increased only slightly by adding superphosphate (1st period), or superphosphate and potash (2nd period), to the dung: more by adding nitrogen compounds, and still more by adding nitrogen, phosphate, and potash; the average yield then rises to almost 30 tons per acre, the highest on the field (Table 1).

The small effect of additional superphosphate indicates that the 100 lb. per acre of P_2O_5 supplied by the farmyard manure are adequate; the limit to yield is set by the other nutrients, for addition of nitrogen and potash greatly increases the yield, although the dung supplies 200 lb. N and 250 lb. K_2O per acre. The responses to farmyard manure are given in Table 6.

TABLE 6. *Increase of Yield of Roots, produced by Farmyard Manure (14 Tons per Acre), in Absence and Presence of Other Fertilizers, Barnfield; Tons per Acre*

	Plots concerned		*Nitrogenous fertilizer*				
			None O	*Sulphate of ammonia A*	*Nitrate of soda N*	*Rape cake C*	*Rape cake and sulphate of ammonia AC*
No minerals	1–8	1876–94	12·99	16·09	12·96	13·44	14·42
	1–8	1904–40	14·39	16·35	17·44	14·70	15·74
P	2–5	1876–94	11·99	13·06	8·53	11·33	12·30
PK	2–6	1904–40	16·17	12·37	12·53	10·20	7·45

In absence of potash the farmyard manure exerts its full effect whether additional nitrogen is supplied or not: its effectiveness is not lowered, indeed it tends to be raised, by addition of sulphate of ammonia or rape cake. This is a remarkable result, for if farmyard manure acted merely as a source of nitrogen it would be expected that the 200 lb. of nitrogen in the farmyard manure would lose effectiveness when augmented by a further 86 lb. supplied as sulphate of ammonia, and still more when 184 lb. is added as rape cake and sulphate of ammonia. But there is no doubt about the result, and it is obtained with potatoes also.

In presence of potash, however, the effect of the farmyard manure is no longer purely additive, it decreases with increasing nitrogen supply. The extra yield produced by farmyard manure when rape cake and sulphate of ammonia are also added is, in presence of potash, only one-half of what it is when no potash or phosphate is supplied; the total yield is 6 tons higher, but it is still short by 8 tons per acre of what would be expected from an additive relation. This falling off from the additive relation in presence of potash and phosphate does not occur with potatoes.

Conversely, the addition of farmyard manure, in the absence of

potash, does not reduce the effectiveness of the nitrogenous fertilizers; on the other hand, it tends to increase the responses to nitrogen especially when phosphate is also lacking. But when potash is given farmyard manure considerably reduces the effectiveness of nitrogenous fertilizers (Table 7).

TABLE 7. *Increase of Yield of Roots, produced by Nitrogenous Fertilizers in Absence and Presence of Farmyard Manure, Phosphate and Potash, Barnfield; Tons per Acre*

Effect of		*In presence of*			
		O	P	FYM	FYM+P
Sulphate of ammonia	1876–94	2·24	3·28	5·34	4·35
Nitrate of soda		6·47	10·68	6·44	7·22
Rape cake		6·41	6·94	6·86	6·28
Rape cake and sulphate of ammonia		6·30	6·14	7·73	6·45
		O	PK	FYM	FYM+PK
Sulphate of ammonia	1904–40	2·61	10·75	4·57	7·95
Nitrate of soda		7·56	13·07	10·61	9·43
Rape cake		5·29	13·79	5·60	7·82
Rape cake and sulphate of ammonia		4·47	18·24	5·82	9·52

In sharp contradistinction to nitrogen, the responses to phosphate and to potash are lowered by farmyard manure (Table 8).

TABLE 8. *Increase of Yield of Roots produced by Phosphate and Potash in Absence and Presence of Farmyard Manure and Nitrogenous Fertilizers, Barnfield; Tons per Acre*

Effect of		*No* N	*In presence of*			
			Sulphate of ammonia	*Nitrate of soda*	*Rape cake*	*Rape cake and sulphate of ammonia*
P 1876–94	No FYM	1·24	2·28	5·45	1·77	1·08
	FYM	0·24	−0·75	1·02	−0·34	−1·04
PK 1904–40	No FYM	0·77	8·91	6·28	9·27	14·54
	FYM	2·55	4·93	1·37	4·77	6·25

These relations are set out in Fig. 3.

The remarkable behaviour of farmyard manure towards nitrogenous fertilizers is attributable to the fact that it supplies potash as well as nitrogen, and this appears to be its more important nutritional effect, for except when potash is also applied it behaves like a potassic fertilizer. In presence of potash, however, it shows the characteristics of a nitrogenous fertilizer.

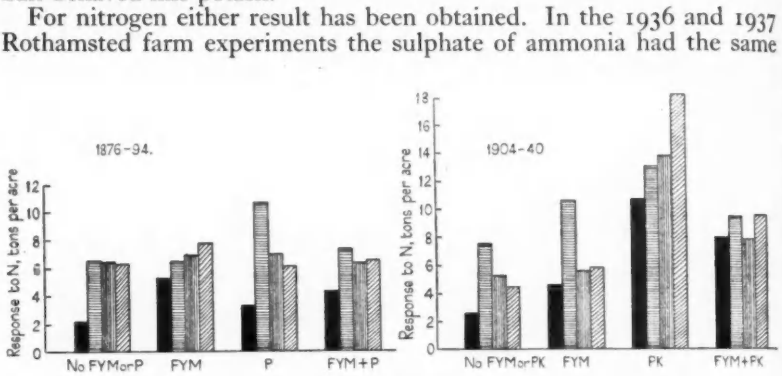
A reduction in effectiveness of potash in presence of farmyard manure was obtained in the Rothamsted farm experiments in 1936 and 1937,[1] and also at Oakerthorpe in 1933 and 1934,[2] where the potash gave only

[1] *Rothamsted Ann. Repts*, 1936, p. 220; 1937, p. 160.

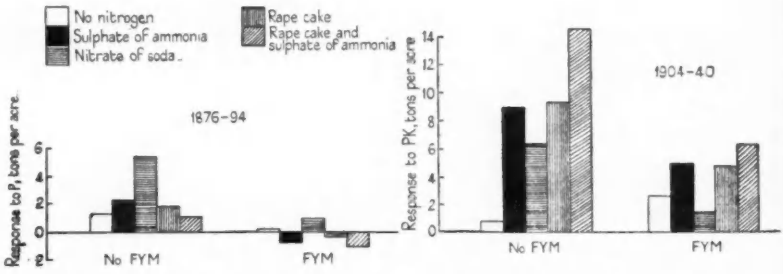
[2] Ibid, 1933, p. 193; 1934, p. 253.

half the return in presence of dung that had been given in its absence. Salt behaved like potash.

For nitrogen either result has been obtained. In the 1936 and 1937 Rothamsted farm experiments the sulphate of ammonia had the same



Effect of farmyard manure on the response to nitrogenous fertilizers in the presence and absence of phosphate or phosphate and potash.



Effect of farmyard manure on the response to phosphate in absence or presence of nitrogenous fertilizers.

Effect of farmyard manure on the response to phosphate and potash in absence or presence of nitrogenous fertilizers.

FIG. 3

effect whether dung was given or not, but in the Oakerthorpe experiments its effect, like that of potash, was greatly reduced by dung.

	Increase of yield, tons per acre, produced by:			
	*Sulphate of ammonia**		*Potash†*	
	Dung absent	*Dung present*	*Dung absent*	*Dung present*
1933	2·28	0·56	4·90	2·44
1934	3·02	1·39	9·26	4·38

* 3 cwt. per acre.

† 30 per cent. potash manure salts, 1·2 cwt. K_2O per acre.

The results suggest a greater liability to interference between dung and sulphate of ammonia for mangolds than exists for potatoes.

Rape cake.—Rape cake has been more effective on mangolds than on either wheat or barley; it has been considerably better than sulphate of ammonia and fully equal to nitrate of soda excepting on the plot receiving superphosphate but no potash. It supplies not only nitrogen, but some 40 lb. P_2O_5 and 20 lb. K_2O per acre, and these help to explain its value.

The yields are given in Table 1, and the responses in Table 9.

TABLE 9. *Increase of Yield of Roots produced by Rape Cake; Tons per Acre*

		In presence of						
		O	P	PK	P Na Mg	PK Na Mg	*Farmyard manure*	*Farmyard manure +P or PK*
Rape cake alone	1876–94	6·41	6·94	13·55	..	15·33	6·86	6·28 (+P)
	1904–40	5·29	5·44	13·79	15·24	16·02	5·60	7·82 (+PK)
Rape cake in presence of sulphate of ammonia	1876–94	4·06	2·86	8·45	..	2·39	2·39	2·10 (+P)
	1904–40	1·86	2·04	7·49	5·36	1·25	1·25	1·57 (+PK)

The response to rape cake, like that to sulphate of ammonia (Table 2), is much increased by adding potash or soda, but it is decreased by adding sulphate of ammonia. It is not, however, affected by adding farmyard manure unless potash and phosphate are present, in which case it is much reduced.

The lowering of the response to sulphate of ammonia brought about by the addition of rape cake is shown in Table 10.

TABLE 10. *Effect of Rape Cake on the Response to Sulphate of Ammonia*

		O	P	PK	P Na Mg	PK Na Mg
Sulphate of ammonia alone	1876–94	2·24	3·28	9·23	..	10·17
	1904–40	2·61	2·79	10·75	12·19	10·87
Sulphate of ammonia in presence of rape cake	1876–94	−0·11	−0·80	4·13	..	4·35
	1904–40	−0·82	−0·61	4·45	2·31	5·78

Rape cake, like sulphate of ammonia, raises the effectiveness of potash and soda (Table 5).

In all these respects rape cake behaves like a nitrogenous and unlike a potassic fertilizer: unlike also farmyard manure.

In several important respects, however, rape cake behaves differently from sulphate of ammonia. It leaves a perceptible residue in the soil. During the four years 1917 to 1920 rape cake was unobtainable, and so had to be withheld from series C and AC: the other fertilizers were, however, given. For the five years 1912–16 the yield on the rape-cake plots without farmyard manure had been about 5 tons greater than on those receiving sulphate of ammonia (Fig. 4). In 1917, the first year in which the rape cake was withheld, the yield was almost the same as on

the sulphate of ammonia plots, but subsequently it fell below. Throughout the five-year period, however, the yield on the rape-cake plots remained much above that on the plots without nitrogen, showing that residues still persisted after four years. Similarly the yield of the AC series (sulphate of ammonia and residues of rape cake) remained above

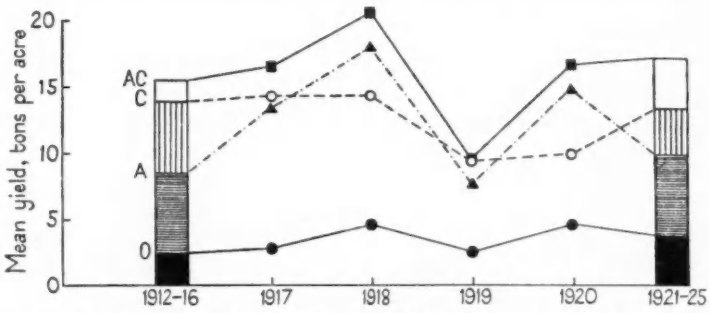


FIG. 4. Residual effect of rape cake, Barnfield. Comparison of the yields of Series O (no nitrogen), Series A (sulphate of ammonia), Series C (rape cake), and Series AC (rape cake and sulphate of ammonia) for the years 1917–20, when rape cake was not given, and the preceding and succeeding five-yearly periods. Mean yield of plots 4, 5, 6, 7, and 8 for each series.

the level of the A series (sulphate of ammonia only), although the difference between the two was less than in the preceding and succeeding periods when rape cake was given.

The conditions are abnormal in that rape cake had been given to the same plots for 61 years in succession at the rate of 2,000 lb. per acre. In an earlier experiment on Barnfield where only six successive dressings were given (1845 to 1850), there was also a perceptible residual effect, but none from the single dressings given in the Little Hoosfield experiments.[1]

Effectiveness of the Different Forms of Nitrogen

The effectiveness of the nitrogen supplied by the different nitrogenous fertilizers is best assessed in the presence of potash and phosphate, for this eliminates the beneficial effects of the potash supplied by rape cake and dung and the soda supplied by nitrate of soda. Allowance can be made for the varying quantities of nitrogen supplied by the different fertilizer dressings by calculating the increase of yield per lb. of nitrogen per acre, but this takes no account of the fact that the effectiveness of nitrogenous fertilizers decreases with increase in the rate of application. A fair comparison is afforded by the responses to a standard dressing of nitrogen (0·25 cwt. per acre), calculated by use of the standard response-curve given by Crowther and Yates.[2] The results of both methods of comparison are shown in Table 11.

[1] D. J. Finney, *Empire J. Expt. Agric.*, 1940, **8**, 111–25.
[2] E. M. Crowther and F. Yates, ibid., 1941, **9**, 77–97.

TABLE 11. *Comparison of the Effectiveness of Different Nitrogenous Fertilizers in increasing the Yield of Mangold Roots, in Presence of Potash and Phosphate, Barnfield*

	Mean Increases of yield, 1904–40				*Calculated response*	
	lb. N *supplied per acre*	*Tons per acre*	*Tons per lb.* N	*Relative effectiveness*	*Tons per acre per 0·25 cwt.* N *per acre*	*Relative effectiveness*
Nitrate of soda	86	13·07	0·152	100	7·17	100
Sulphate of ammonia	86	10·75	0·125	82	5·89	82
Rape cake	98	13·79	0·141	93	7·28	102
Farmyard manure	200	16·17	0·081	53	3·72	52

Rape cake and nitrate of soda are both more effective sources of nitrogen than sulphate of ammonia, and when the comparison is based on the values calculated from the response-curve, rape cake is as effective as nitrate of soda. In the early years of the experiment rape cake was superior to nitrate of soda; the effectiveness of its nitrogen relative to that of nitrate of soda as 100, when the comparison is made on the response-curve basis, was 118 for the period 1876–94. The relative effectiveness of nitrate of soda and sulphate of ammonia was almost identical in the two periods, and very similar values are obtained if the comparison is made in the presence of soda and magnesia as well as potash and phosphate.

The nitrogen in farmyard manure was only half as effective as that in nitrate of soda, and the same value is obtained whichever method of calculation is used, in spite of the wide difference in quantities of nitrogen supplied by the two materials. The reason is that the response to additional farmyard manure declines much less rapidly with increase in the quantity applied than does the response to nitrate of soda or sulphate of ammonia, presumably because farmyard manure has beneficial effects additional to those attributable to increase in the supply of nitrogen.

Table 12 shows the responses on Barnfield, converted to the standard

TABLE 12. *Increase in Yield of Mangold Roots produced by 0·25 cwt.* N *per Acre, or 10 Tons per Acre of Farmyard Manure; Tons per Acre*

Nitrogenous fertilizers	*In absence of farmyard manure*	*In presence of farmyard manure*
Barnfield		
Nitrate of soda	7·2	5·2
Sulphate of ammonia	5·9	3·8
Rape cake	7·3	4·1
Average for rotation crops	3·1	2·6
Farmyard manure	*In absence of* N, P, *or* K	*In presence of* NPK
Barnfield	11·9	10·3
Average for rotation crops	7·7	2·7*

* In presence of fertilizers, not necessarily complete artificials.

dressings of 0·25 cwt. N per acre or 10 tons of dung per acre by means of the response-curve, and also the average values given by Crowther and Yates for mangold crops grown in rotation in Great Britain.

The responses on Barnfield are all much greater than the average values for rotation crops, presumably because of the exhaustion of the plots which have received no nitrogenous fertilizer or dung for many years. It is also noteworthy that, on Barnfield, farmyard manure has given almost as great an increase of yield when applied in the presence of a complete fertilizer dressing as when applied alone, whilst in the rotation experiments it gave much less increase in presence of fertilizers.

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THE ROTHAMSTED EXPERIMENTS ON MANGOLDS, 1872–1940

PART II. EFFECT OF MANURES ON THE GROWTH OF THE PLANT

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Effect of manurial treatment on the survival of mangold plants.—The plants have been counted on every plot of Barnfield just before harvest each year since 1901[1]; the mean plant numbers per acre are shown in Table 1.

The crop is sown in rows 26 in. apart, and in thinning a spacing of 10 in. in the rows is aimed at, corresponding to approximately 24,000 plants per acre. The mean plant-population of all plots, however, was 15·8 thousands, so that on the average only two-thirds of a perfect stand was

TABLE 1. *Mean Plant-number; thousands per acre (1901–40; 35 years, omitting 1908, 1927, 1930, 1931, 1935)*

	Farmyard manure		*No farmyard manure*					
	No minerals	PK	*No minerals*	P	PK	P Na Mg *No* K	P Na Mg K	Mean
Series	1	2	8	5	6	7	4	
O	15·8	16·2	15·0	15·9	15·6	16·0	16·1	15·8
N	15·8	15·5	15·1*	14·6*	15·1*	15·7*	A 15·4* B 15·6†	15·3
A	16·2	16·0	14·2*	14·0*	14·9*	15·6*	15·3*	15·2
AC	16·5	16·8	15·5	15·5	15·8	16·4	15·9	16·1
C	16·7	17·2	16·5	16·6	16·5	16·8	16·7	16·7
Mean	16·2	16·3	15·3	15·3	15·6	16·1	15·9	15·8

* 34 years, 1904 omitted. † 32 years, from 1904.

achieved; the actual average spacing in the rows was therefore about 15 in. The dunged plots had the highest mean plant-number, and the further addition of phosphate and potash was almost without effect.

Rape cake also increased the plant number; on the other hand, both nitrate of soda and sulphate of ammonia slightly reduced it.

Of the mineral fertilizers used without dung, superphosphate seems to be without effect. Potash has a small beneficial effect when applied with sulphate of ammonia or nitrate of soda in the absence of soda and magnesia. The mixture of salt and sulphate of magnesia, on the other hand, is consistently beneficial. The magnitude of its effect also is influenced by the nitrogenous fertilizer: with sulphate of ammonia the beneficial effect is particularly marked; with nitrate of soda it is less; and with rape cake it is scarcely evident. When sulphate of ammonia is

[1] In 1903 some plots of series N and A were omitted.

added to the rape cake, however, the beneficial effect of soda and magnesia is shown. Plant-number is thus lowest on the plots receiving sulphate of ammonia and superphosphate only, and highest on those receiving farmyard manure and rape cake, or rape cake, soda, and magnesia.

It is difficult to say which constituent of the salt and sulphate of

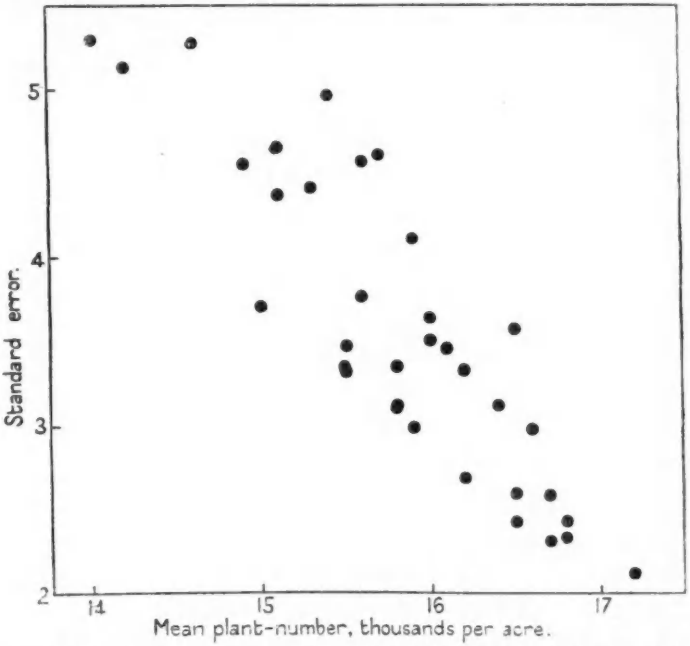

FIG. 1. Relation between the seasonal variability of plant-number, as measured by the standard error for a single year, and mean plant-number for the plots of Barnfield.

magnesia mixture is the effective one in raising plant-number. Apparently it is not the sodium, for (*a*) the mixture, though supplying only about 100 lb. Na_2O per acre has been much more effective than 200 lb. Na_2O supplied as nitrate of soda, and is effective when given in the presence of nitrate of soda; and (*b*) the substitution of calcium for sodium (4NB compared with 4NA) has had no effect on mean plant-number. As there is no reason why magnesium should have any specific action it seems simplest to regard the chloride ion as the effective agent.

The good effects of rape cake and of dung cannot be attributed to the nutrients present. The 200 lb. nitrogen supplied by dung and the 9[illegible] lb. supplied by the rape cake would indeed be expected to reduce plant-number, and this effect would probably not be offset by the potash present. The beneficial effect can therefore be attributed to the organic matter, which, as shown later, modifies the physical texture of the soil (p. 76).

Seasonal variation of plant number.—The variability in plant-number from year to year is greater on the plots with high mean numbers than with low ones (Fig. 1). This arises from the circumstance that an upper limit is set to the plant-number by the thinning, and so a high mean value is possible only when the numbers vary but little from the maximum; but a high variability means that low values must have occurred frequently, resulting in a lower mean value. This is illustrated in Fig. 2, where the frequency distribution of plant-number in different seasons is compared for plots with high and low mean plant-numbers.

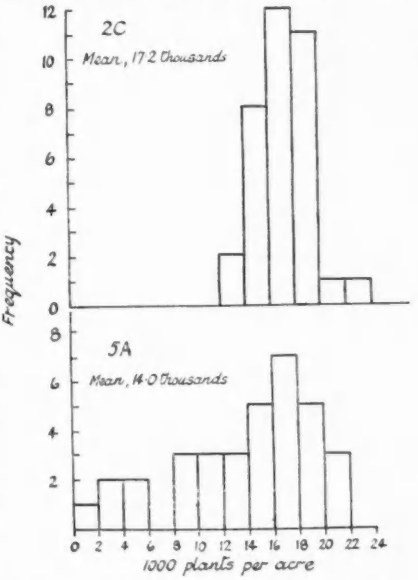

FIG. 2. Frequency distribution of plant-number in thousands per acre in different seasons of the period 1901–40. Plots 2C and 5A, Barnfield.

Relation between plant-number and yield.—High plant-number goes with high yield; indeed for some of the plots the differences in yield are due almost entirely to differences in plant-number, the average weight per root (Table 2) being approximately constant, e.g. 4–0, 5–0, 6–0 and 7–0 (effect of potash or of soda and magnesia in absence of nitrogen); 5 N and 6 N (effect of potash in presence of nitrate of soda); here the potash has not increased the size of root but only the survival of plants. Usually, however, the fertilizer has affected both weight of root and extent of survival, but the latter is for all plots an important factor in the final yield; the regression coefficients of yield on plant-number (Table 2) are all positive and with only one exception (plot 2–0) significant. The relation between yield and plant-number is adequately expressed by a straight line: this is shown by the fact that the quadratic regression coefficients are small and not significant.

Competition between plants.—The closeness of the connexion between plant-number and yield depends on the amount of competition between the plants. If there is no competition, yield is proportional to the plant-number. If competition is very severe the removal of some of the plants enables the survivors to make more growth, thus compensating somewhat for the reduction in number. An appropriate measure with which to compare the degree of competition on different plots can be calculated from the data given in Table 2. The regression coefficients represent the average loss of yield resulting from the elimination of 100 plants. If there were no competition between plants, this loss of yield would be equal to the average yield of 100 plants, but wherever competition occurs, it is less than the yield of 100 plants, the difference increasing as

competition becomes more intense. In Table 3 the regression coefficient is expressed as per cent. of the mean yield of 100 roots. This quantity, called *k* for convenience, is a measure of the independence of growth of, or absence of competition between, the roots; that is, an increase in the

TABLE 2. *Regression Coefficients of Yield of Roots in cwt. per acre on Plant-number in hundreds per acre, and the Mean Weight per 100 Roots in cwt.*

Series		Strip 1	2	4	5	6	7	8
O	Regression coefficient	1·43 ±0·50	1·06 ±0·76	0·44 ±0·15	0·49 ±0·13	0·32 ±0·14	0·34 ±0·15	0·30 ±0·11
	Weight per 100 roots, cwt.	2·17	2·42	0·52	0·50	0·48	0·50	0·40
N	Regression coefficient	2·31 ±0·70	2·79 ±0·82	2·25 ±0·43	2·04 ±0·31	2·05 ±0·41	1·92 ±0·48	1·58 ±0·34
	Weight per 100 roots, cwt.	3·49	3·71	2·42	2·15	2·19	2·30	1·37
A	Regression coefficient	2·21 ±0·56	2·81 ±0·68	1·38 ±0·46	1·07 ±0·19	1·52 ±0·40	1·45 ±0·44	0·89 ±0·17
	Weight per 100 roots, cwt.	2·70	3·34	1·98	0·95	1·91	2·02	0·78
AC	Regression coefficient	2·97 ±0·72	3·08 ±1·01	1·77 ±0·82	1·30 ±0·56	2·57 ±0·70	2·33 ±0·74	1·21 ±0·30
	Weight per 100 roots, cwt.	2·83	3·54	3·34	1·14	2·83	2·68	0·99
C	Regression coefficient	2·69 ±0·65	2·84 ±0·97	2·37 ±0·86	1·52 ±0·41	3·08 ±0·71	2·93 ±0·81	1·38 ±0·33
	Weight per 100 roots, cwt.	2·78	3·25	2·51	1·15	2·17	2·31	1·03

TABLE 3. *Regression Coefficients of Yield of Roots in cwt. per acre on Plant-number in hundreds per acre, as per cent. of Mean Weight of 100 Roots (k)*

	Farmyard manure		*No farmyard manure*					
Series	*No minerals* 1	PK 2	P Na Mg K 4	P 5	PK 6	P Na Mg *No* K 7	*No minerals* 8	*Mean*
O .	66	44	86	98	67	68	75	72
N .	66	75	93	95	94	83	115	89
A .	82	84	70	112	80	72	115	88
AC .	105	87	53	114	91	87	123	94
C .	97	88	94	132	142	127	134	116
Mean .	83	76	79	110	95	87	112	92

intensity of competition causes a decrease in *k*. A value of 100 denotes a complete absence of competition, changes in plant-number causing a proportionate increase in yield, whilst a value of zero indicates such intense competition that complete compensation occurs for changes in plant-number, and yield is independent of plant-number. A value of 60, for example, means that the elimination of 100 plants causes a loss of only 60 per cent. of the weight of 100 roots, the degree of competition being such that increased growth of the remaining plants compensates to the extent of 40 per cent. for the missing plants.

Some of the values in Table 3 exceed 100, probably because in some seasons weather conditions favour both growth and plant-survival, so that yield and plant-number both tend to be high, leading to an over-estimation of the regression coefficients. This suggests that all of the values in the table are too high.

The mean value for all the plots, 92 per cent., shows that in general there is little competition on Barnfield. For other series of British, Danish, and Dutch experiments on mangolds and sugar-beet, Finney[1] obtained lower values ranging from 45 to 62, indicating greater competition. The difference is probably due to the higher plant-density in these experiments, the mean value in different series ranging from 21 to 25 thousands per acre as against 16 thousand on Barnfield. Finney showed that over the wide range of plant-population which occurred in these experiments, the intensity of competition increased with increase in plant-density.

There is no close relation between competition, as measured by k, and mean plant-number per acre on the different plots of Barnfield, probably because the range of plant-density is small. It follows that the effects of manurial treatment on competition, discussed in the next section, are independent of the effect of the manures on mean plant-number.

Effect of manurial treatment on competition.—The value of k is increased by the addition of sulphate of ammonia or nitrate of soda, and especially by rape cake, but sulphate of ammonia given in the presence of rape cake causes a slight reduction. It is lowered by potassic fertilizer and still more by the mixture of salt and magnesia; also by dung, especially when potash and phosphate are given in addition. Phosphate had little effect. An increased supply of nitrogen thus reduces competition, whilst an increased supply of alkali salts or of dung intensifies it. Assuming that competition for a nutrient is greatest when the supply is low, it follows that mangolds in the Broadbalk soil compete only for nitrogen and not for potash or soda; this is confirmed by the absence of competition on the plots without potash or soda so long as they have adequate nitrogen (strips 5 and 8).

Within each series of plots receiving the same nitrogen supply competition increases with increasing yield. This is shown by the regression coefficients of k on yield (Table 4). All are negative and all significant or bordering on significance.

TABLE 4. *Linear Regression Coefficients of k on Yield of Roots in cwt. per acre*

Series . .	*O*	*N*	*A*	*AC*	*C*
	−0·083 ±0·038	−0·113 ±0·019	−0·080 ±0·040	−0·104 ±0·038	−0·123 ±0·045

This suggests that the mineral fertilizers, which cause the differences in yield between the plots within each nitrogen series, intensify competition

[1] D. J. Finney, this journal, 1941, **9**, 57–64.

merely by increasing the yield, and so increasing the ability of the plants to take up nitrogen. There is no evidence of any specific effects of the mineral fertilizers independent of their effect on yield, for the deviations from the regression lines are not consistently of the same sign for all plots of each strip receiving the same mineral fertilizers.

No such relation between competition and yield exists within each strip of plots receiving the same mineral fertilizers; instead, the increase of yield caused by nitrogenous fertilizers is associated with a decrease in competition, but the relation between k and yield is not close.

These results show that considerable compensation takes place around a gap if the supply of potash or soda is adequate but that of nitrogen is not, presumably because plants surrounding a gap are able to obtain an increased supply of nitrogen. But in the reverse condition of ample nitrogen supply but deficiency of potash or soda there is little or no compensation. The reason for this is not clear, but the results seem to imply either that the presence of a gap does not increase the supply of potash or soda to plants surrounding it, or, if it does, the increased uptake of potash or soda does not affect the growth of the plants. Incidentally, these results explain why edge effects are so much more pronounced on the plots without added nitrogen than on those without added potash or soda.

It is difficult to understand this difference between the effects of nitrogen and potash seeing that both are essential for growth. Competition for nutrients presumably does not occur until a fairly late stage of growth when the root-systems have developed sufficiently to explore all the soil between the plants, and it may be that potash or soda assimilated late is less effective than that assimilated early but that nitrogen is effective whenever it is taken up. Alternatively there may be some difference in the process of uptake which causes the difference.

Table 3 brings out an interesting difference between rape cake and dung. Rape cake behaves like a nitrogenous fertilizer in reducing competition, whilst dung behaves like potash and soda in increasing it. The explanation is given by the amounts of nutrients supplied; they are, approximately, in lb. per acre:

	N	K_2O
Dung . .	200	250
Rape cake . .	100	20

The dung supplies much more potash than the rape cake, and although its nitrogen is double in amount it has only half the effectiveness (Table 6, Part 1).

Effect of varying the width between rows.—The usual spacing of the rows on Barnfield is 26 in. In 1930 a comparison was made of two spacing widths, one half of each plot being sown at the normal spacing and the other half at 20 in. The results are given in Table 5. As the test was made for only one season, the yields of individual plots are subject to large errors, and accordingly only the means for the series of plots receiving different nitrogenous fertilizers and for the strips receiving different mineral fertilizers or farmyard manure are given.

TABLE 5. *Increase of Yield of Roots in tons per acre, and of Plant-number in thousands per acre, produced by Narrow Spacing of the Rows (20 in.), compared with the Normal Spacing (26 in.). Barnfield, 1930*

(*a*) *Effect of nitrogenous fertilizers* * (*average of mineral fertilizer treatments*)

	Series . . .	*O*	*A*	*AC*	*C*	
	Nitrogenous fertilizers	*No nitrogen*	*Sulphate of ammonia*	*Sulphate of ammonia and rape cake*	*Rape cake*	*Mean*
Yield	Normal spacing . .	5·49	11·91	18·08	14·79	12·57
	Increase with narrow spacing . . .	0·25	1·70	1·63	1·97	1·39
	Increase, per cent. .	4·5	14·3	9·0	13·3	11·1
Plant number	Normal spacing . .	12·5	8·5	12·6	12·8	11·6
	Increase with narrow spacing . . .	3·5	2·2	3·1	4·1	3·2
	Increase, per cent. .	28·0	25·9	24·6	32·0	27·6

* Series N omitted, as the produce of normal and narrow-spaced rows was bulked on plots 5, 6, and 8 owing to low yield, and the two halves of plot 4 N receive different treatments (see Part I, p. 56).

(*b*) *Effect of mineral fertilizers and dung* (*average of nitrogen treatments*)

	Strip	*1*	*2*	*4*	*5*	*6*	*7*	*8*	
	Mineral fertilizer . .	*Farm-yard manure*	*Farm-yard manure*	PK Na Mg	P	PK	P Na Mg	*None*	*Mean*
Yield	Normal spacing . .	13·14	15·12	16·19	7·85	14·18	14·27	7·21	12·57
	Increase with narrow spacing	2·64	−0·02*	0·60	0·99	2·06	2·09	1·36	1·39
	Increase, per cent. . .	20·1	−0·1	3·7	12·6	14·5	14·6	18·9	11·1
Plant number	Normal spacing . .	13·9	10·8	12·4	11·4	11·1	10·7	11·1	11·6
	Increase with narrow spacing	0	3·0	1·2	5·3	3·5	5·4	4·1	3·2
	Increase, per cent. . .	0	27·8	9·7	46·5	31·5	50·5	36·9	27·6

* A negative sign indicates that narrow spacing gave a lower yield than normal spacing.

The average increase in the number of plants per plot given by the narrow spacing was 28 per cent., which corresponds closely with the 30 per cent. increase which would be obtained if the average spacing of the plants in the row was the same for both spacings of the rows. The average increase in the yield of roots was only 11 per cent., showing that competition was severe. The value of k, which represents the average increase of yield per additional plant as per cent. of the mean yield per plant, calculated from these results is 40 per cent. This is very much less than the mean value, 92 per cent. (Table 3), obtained from the relation between yield and plant-number in different seasons, in which the spacing of the plants in the row varied, the spacing of the rows being kept constant. The inference that competition between rows is more intense than within rows can scarcely be accepted, for since neighbouring

plants in the same row are closer together than neighbouring plants in adjacent rows, the reverse would be expected. It is known that the values of k given in Table 3 are probably too large, but they are unlikely to be twice as great as the true values. It is possible that competition was especially severe in 1930, and that if the comparison of row-spacings was made over a period of years a much higher average value of k would be obtained, but this explanation does not accord with the fact that the yields in 1930 were much below average.

The effect of manurial treatment on competition, as shown by the increase of yield produced by the narrower spacing, agrees fairly well with that shown by the values of k in Table 3. Sulphate of ammonia and rape cake applied separately reduced competition, as shown by the greater increase of yield given by the narrower spacing, on the strips which received these fertilizers, than on the no-nitrogen strip. As in Table 3, however, sulphate of ammonia applied in the presence of rape cake apparently reduced competition.

The effect of potash and soda was less consistent. The narrower spacing increased yield less on strip 4 (PKNaMg) than on strips 6 (PK) and 7 (PNaMg), and on strip 8 (no minerals) the relative increase was greater than on the other strips. These comparisons show that potash and soda increased competition. Strip 5 (P) is anomalous, however, for the relative increase of yield was smaller than on strips 6 and 7, indicating that potash or soda applied separately reduced competition. The small increase on strip 5 was largely due to the fact that on plot 5C narrow spacing gave a lower yield than the normal spacing, and if this plot is omitted the discrepancy disappears and on the remaining plots potash and soda increased competition.

The results for the farmyard-manure strips are also somewhat anomalous. On strip 1 (farmyard manure alone) the narrower spacing did not increase plant-number, but gave a considerably higher yield than the normal spacing. Apparently the change in distribution of the plants with the narrower spacing, which gave a more nearly square arrangement without altering plant-number per acre, itself reduced competition, presumably by giving a better utilization of the soil. On strip 2 (farmyard manure and PK), on the other hand, the narrower spacing increased plant-number by 30 per cent. but did not increase the yield; apparently competition was so severe that complete compensation for variation in plant-number occurred. This is in agreement with Table 3, which also shows that competition was more intense on strip 2 than on the other strips receiving farmyard manure or mineral fertilizers.

Yield of leaves, and its relation to the yield of roots.—The mean yields of leaves at harvest, for the period 1904–40 since the final changes were made in the manurial treatments, are shown in Table 6.

The yield of leaf depends almost entirely on the supply of nitrogen, and is very little affected by the mineral fertilizers. In the absence of farmyard manure, nitrate of soda and sulphate of ammonia supplying 86 lb. N per acre, and rape cake supplying 98 lb. N per acre have, on the average, increased the yield from 1 ton per acre without nitrogen to 3 tons per acre. Rape cake and sulphate of ammonia, supplying together

TABLE 6. *Mean Yield of Leaves, tons per acre. Barnfield, 1904–40*

		No farmyard manure						*Farmyard manure*		
	Minerals . .	*None*	P	PK	PNaMg	PKNaMg	*Mean*	*None*	PK	*Mean*
	Strip . . .	*8*	*5*	*6*	*7*	*4*		*1*	*2*	
Series	*Source of nitrogen*									
O	No nitrogen . .	1·0	1·0	1·0	1·1	1·1	1·0	3·3	3·5	3·4
A	Sulphate of ammonia	2·6	2·6	3·0	3·3	3·2	2·9	4·9	5·7	5·3
N	Nitrate of soda .	3·4	3·4	3·4	3·8	(A) 4·1	3·6	5·0	5·6	5·3
C	Rape cake . .	2·8	2·9	3·0	3·6	3·5	3·2	4·8	5·4	5·1
AC	Rape cake and sulphate of ammonia	3·0	3·1	5·2	5·2	5·5	4·4	5·1	6·5	5·8
	Mean . .	2·6	2·6	3·1	3·4	3·5	3·0	4·6	5·3	5·0

184 lb. N, have caused a further increase to between 4 and 5 tons per acre.

Superphosphate applied alone has had no detectable effect on the yield of leaves. Potash has given an additional 0·5 ton of leaf per acre, and the response to salt and sulphate of magnesia was slightly greater, 0·8 ton on the average. There is evidence of a negative interaction between potash and salt; when applied together these fertilizers were less effective than when applied separately. The responses to potash and salt depend on the level of nitrogen supply. In the absence of nitrogen, potash and salt have had no effect, whilst the responses have been greater on series AC, which receives 184 lb. N per acre as rape cake and sulphate of ammonia, than when 86 lb. N is given as sulphate of ammonia or nitrate of soda, or 98 lb. N as rape cake.

Farmyard manure has consistently increased the yield of leaf by about 2 tons per acre, whether given alone or in the presence of artificial fertilizers. Conversely, it follows that the effects of the nitrogenous fertilizers, and of phosphate and potash applied together, are almost independent of the presence or absence of farmyard manure.

The results for the earlier years of the experiment were similar.

Table 7 shows the effect of manurial treatment on the ratio of the yield of roots to the yield of leaves.

The ratio is smallest for the plots which received no mineral fertili-

TABLE 7. *Ratio of Mean Yield of Roots to Mean Yield of Leaves. Barnfield, 1904–40*

		No farmyard manure						*Farmyard manure*		
	Minerals . .	*None*	P	PK	PNaMg	PKNaMg	*Mean*	*None*	PK	*Mean*
	Strip . . .	*8*	*5*	*6*	*7*	*4*		*1*	*2*	
Series	*Source of nitrogen*									
O	No nitrogen . .	3·0	4·0	3·8	3·6	3·8	3·6	5·3	5·7	5·5
A	Sulphate of ammonia	2·2	2·6	4·8	4·9	4·8	3·9	4·5	4·7	4·6
N	Nitrate of soda .	3·1	4·7	5·0	4·9	(A) 4·6	4·5	5·6	5·2	5·4
C	Rape cake . .	3·0	3·3	5·8	5·3	5·9	4·7	4·8	5·1	5·0
AC	Rape cake and sulphate of ammonia	2·5	2·9	4·2	4·1	4·8	3·7	4·5	4·5	4·5
	Mean . .	2·8	3·5	4·7	4·6	4·8	4·1	4·9	5·0	5·0

zers, especially where sulphate of ammonia was given. Phosphate increased the ratio, and the further addition of potash or soda and magnesia increased it still more, except in the absence of nitrogenous fertilizer. The effect of potash and soda on the ratio was less, and that of phosphate greater, in the presence of nitrate of soda, than where the other nitrogenous fertilizers were given. These results show that potash and soda, and to a less extent phosphate, had a relatively greater effect on the yield of roots than on the yield of leaves.

The effect is more obvious if the actual yields of leaves and roots are compared. For example, potash given in the presence of sulphate of ammonia and phosphate increased the yield of leaves only from 2·6 to 3·0 tons per acre, but the yield of roots increased from 6·8 to 14·5 tons per acre. Equally striking effects were produced by the mixture of sodium and magnesium salts, and on the rape-cake plots. The physiological explanation of this result is complex, and it is not justifiable to attribute the result solely to an increase in rate of assimilation per unit weight of leaf by the mineral fertilizers. During the later stages of growth, the older leaves die off, so that differences between plots in the leaf-weight of the crop during the time when the crop is growing most actively are not necessarily closely related to the differences in the final leaf-weight at harvest.

The ratio was also increased by nitrogenous fertilizers, except sulphate of ammonia in absence of potash or soda. The average effect of sulphate of ammonia on the ratio was small, compared with those of potash and soda. Nitrate of soda and rape cake had a greater effect, probably by virtue of the soda and potash which they supply.

Farmyard manure increased the ratio of root to leaf when applied alone, but in the presence of potash and phosphate it had little effect, except on the no-nitrogen strip. The ratio varied little for the plots which received farmyard manure, showing that both nitrogenous and mineral fertilizers increased the yield of leaf and root almost proportionately when applied in the presence of farmyard manure.

The ratio of root to leaf was greater in years of high yield than in years of low yield. Table 8 gives the regression coefficients of the root/leaf ratio on the yield of roots, for a number of plots selected to cover a wide range of fertilizer treatments and mean yield. All the coefficients are positive and highly significant. It follows that the yield of leaf is relatively less variable between seasons than the yield of roots. Also, variation in the supply of nitrogen from the soil is unlikely to be a major factor in causing seasonal variation, for changes in the supply of nitrogen have little effect on the ratio of root to leaf.

Bolting.—Although the mangold normally behaves as a biennial, occasionally it flowers during the first year of growth. This is called 'bolting', and it is disliked by farmers because it is considered, probably correctly, to reduce the feeding-value of the root. Plants which bolt presumably differ genetically from those which do not. The proportion of bolters on Barnfield is usually very small; the highest percentage recorded on any plot was 2·7 (on plot 2C in 1932), and in many seasons there have been none.

TABLE 8. *Regression Coefficients of Ratio of Yield of Roots to Yield of Leaves, on Yield of Roots. Barnfield, 1876–1939 (59 years)*

Plot	*Treatment*	*Mean yield of roots, tons per acre*	*Mean root: leaf ratio*	*Regression coefficient of root: leaf ratio on mean yield of roots*
8–O	Unmanured	3·31	3·37	0·78±0·072
4–O	PK Na Mg	4·62	4·38	0·62±0·083
4Na	N PK Na Mg	17·83	4·55	0·18±0·022
2N	Farmyard manure and NPK	26·91	5·34	0·13±0·020

TABLE 9. *Mean Number of Bolters per Plot, for 16 Years during which Counts were made. Barnfield (1891, 1902, 1916, 1918–19, 1928–30, 1932–4, 1936–40)*

Series	*Strip*							*Mean*
	1	*2*	*4**	*5*	*6*	*7*	*8*	
O	4·1	4·9	0·3	0·2	0·4	0	0·1	1·4
N	10·8	12·0	5·9	6·6	5·0	6·0	0·9	6·7
A	16·4	15·8	5·8	3·2	4·6	4·9	0·4	7·3
AC	19·2	20·4	17·1	6·1	17·9	15·9	2·6	14·2
C	14·1	19·2	12·7	4·8	9·1	8·1	1·7	9·9
Mean	12·9	14·5	8·4	4·2	7·4	7·0	1·1	7·9

* Numbers for plots of strip 4 are calculated to an area equal to that of the other plots.

Fertilizers affect the number of bolters markedly, and consistently from season to season. Table 9 gives the mean number of bolters for each plot, for the 16 years in which counts were recorded.

All fertilizer treatments tend to increase bolting, and the highest numbers therefore occur on plots 2AC, 2C, and 1AC, which receive dung and rape cake in addition to artificial fertilizers, whilst the lowest numbers occur on plots 8–O (unmanured), 5–O (superphosphate only), and 7–O (superphosphate and sulphates of soda and magnesia). There appear to be no marked specific effects of the different nutrients; any improvement in the nutritional status of the crop increases the tendency to bolt, so that there is a close relation between mean yield and bolting (Fig. 3). Of the nitrogenous fertilizers, nitrate of soda has caused slightly more bolting than sulphate of ammonia, except in the presence of dung, where the reverse effect was produced. Rape cake caused more bolting than either sulphate of ammonia or nitrate of soda, but dung had a greater effect than any of the artificial fertilizers. The effects of potash and of the soda and magnesia salts were very similar.

There is large seasonal variation in the number of bolters, but unfortunately the available data are insufficient for an examination of the effects of seasonal weather factors. Until 1928 counts were made rarely and only in years when much bolting occurred, but subsequently they

have been made every year. For the period 1928–40 there is some evidence that early sowing has increased the tendency to bolt. Four of the eleven crops grown during this period had 6 or more bolters per plot, and these were all sown on or before May 1; none of the remaining seven crops had on the average more than 2 bolters per plot, and these were all sown on or after April 30. The regression coefficient of the

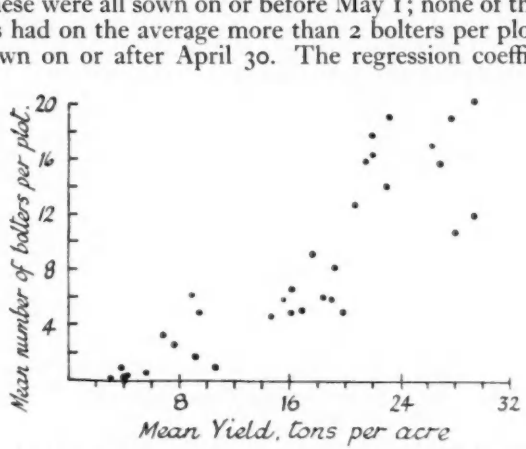

FIG. 3 Relation between mean number of bolters per plot and mean yield of roots, for the plots of Barnfield.

number of bolters per plot on sowing date, $-0{\cdot}649 \pm 0{\cdot}337$ bolters per plot, is not, however, statistically significant; it indicates that a delay of one day in sowing reduces the number of bolters by about 10 per cent. of the mean (6·3 per plot for the period 1928–40). For the closely related sugar-beet crop early sowing is known to be conducive to bolting.

The effects of the fertilizers and manures on the soil.—Barnfield differs from Broadbalk and Hoosfield in that the soil seems to have been physically affected by the nitrate of soda: in difficult seasons, though not in normal ones, it becomes sticky and will not come into a good tilth. The surface soil contains a lower proportion of water-stable crumbs (Table 10) and less clay than on other plots. A. D. Hall[1] attributed the differences to a deflocculating action of the sodium ion on the clay, which is quite probable; the plots are not randomized, however, and there may be inherent differences in the soils themselves. Neither Broadbalk nor Hoosfield soils behave like the Barnfield soils; this may result from the difference in cropping.

Of all the strips No. 5 most readily forms a good tilth on cultivation. It receives superphosphate only and no sodium chloride or sulphate of potash or magnesia; suggesting that all these salts, like nitrate of soda, interfere somewhat with the production of tilth. Hall showed that all of them caused some deflocculation of the clay, presumably by interaction with the calcium carbonate of the soil to form an alkali carbonate.[2]

Rape cake improves the tilth and also increases the proportion of water-stable crumbs (Table 10); in consequence the young plants grow

[1] A. D. Hall, *Trans. Chem. Soc.*, 1904, **85**, 964–71.
[2] A. D. Hall, *J. Roy. Agric. Soc.*, 1909, **70**, 12–35.

more rapidly and survive better than on the plots receiving mineral manures only.

Farmyard manure, however, produces the most striking effects. The soil becomes darker and more friable, and the proportion of water-stable crumbs is higher than on any of the other plots. Contrary to expectation, however, it does not so easily work down to a fine tilth for the seed-bed. Instead it comes to small lumps which, however, are not sticky. Ploughing has in some years been later on the dunged strips than on the others, so that the action of the frost has been missed. The young plants grow more quickly and are sooner ready for singling than on any other plots, and this early start is maintained for a considerable part of the plant's life. It becomes very pronounced in a dry spring, when another property comes into play: the farmyard-manure plots always contain more moisture than the others.[1]

TABLE 10. *Percentage by weight of Soil in Water-stable Crumbs smaller than 4 mm. and larger than ½ mm. (E. W. Russell)*

	Farmyard manure		*No farmyard manure*	
	No minerals	PK	PK Na Mg	P
Series	*1*	*2*	*4*	*5*
N Nitrate of soda . . .	30	23	11	24
A Sulphate of ammonia . .	35	34	17	28
AC Sulphate of ammonia + rape cake	45	36	23	34

[1] See E. J. Russell, *Soils and Manures*. Camb. Univ. Press, 1940, p. 241 for diagram.

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THE BIOLOGICAL CONTROL OF A MEALY BUG ON COFFEE AND OTHER CROPS IN KENYA

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IN 1923 there occurred a severe infestation by the mealy bug *Pseudococcus kenyae* Le Pelley on coffee in the Thika district of Kenya, several features of which are of interest to students of biological control. Firstly, coffee had been grown in the country for more than 20 years without any serious mealy-bug attack; secondly, its extreme severity in the original outbreak centre in Thika, followed by its rapid spread to the adjoining coffee districts of Ruiru, which it appears to have reached the same year, and Kiambu, parts of which it reached not later than 1924, and its subsequent spread to districts farther afield. In Kenya the insect is still confined to a portion of the Central Province stretching from Machakos in the south to Meru in the north. The northward extension of its range on the east side of Mount Kenya has been followed fairly accurately in recent years, and it is known, for example, to have reached just north of Embu by October 1937, Choogoria by June 1938, within 15 miles of Meru by January 1939, and to have been in Meru in April 1939. This form of spread is consistent only with the explanation that the mealy bug is a recent introduction to the area, and this is confirmed by other considerations of which only one need be mentioned here, namely, that no hymenopterous parasites of any importance were associated with the insect in Kenya. If the insect were indigenous, or had it been in the country for a very long time, it is almost certain that it would have had a number of important hymenopterous parasites.

First attempts at biological control.—Some years elapsed before the introduced status of the mealy bug was established, and more still before it was recognized as an undescribed species. In the earliest years it was thought to be *Pseudococcus citri* (Risso) and attempts at biological control were begun as early as 1925, when a collection of material of *Pseudococcus citri* parasitized by *Leptomastidea abnormis* was made in Sicily and sent to Kenya. This introduction was not successful, as no parasites were recovered from the material.

Later, the mealy bug was considered to be *Pseudococcus lilacinus* Ckll., and was referred to by this name until 1934. Efforts at biological control were made by introducing enemies of different mealy bugs, some of which were quite small introductions, but others were more ambitious. Among the latter was the coccinellid *Cryptolaemus montrouzieri* in 1924 and again in 1929. From the second of these introductions more than 100,000 beetles were reared and liberated widely, and though one or two generations were undoubtedly passed in the field, the insect did not become permanently established. Another introduction was of the midge *Schizobremia coffeae*, from Tanganyika, where its larvae are predacious on several mealy bugs. The result of this introduction is not quite certain, except in so far as it is known to have had little economic

effect, for though a midge is now fairly commonly found in clusters of *P. kenyae*, it has not been confirmed that this is the introduced species, nor is it certain that the midge was not present in Kenya before, as an enemy of mealy bugs other than *P. kenyae*. The other project which requires brief mention was a widespread search of the Far East for mealy-bug parasites, particularly those of *P. lilacinus*, which was made in 1936 and 1937, the writer doing the work of exploration and collection whilst the work of testing the insects on *P. kenyae* was in charge of A. R. Melville. A large number of parasites and predators were obtained and successfully shipped, many from far-distant countries, notably the Philippine Islands and Java. None of the primary parasites of *P. lilacinus* could be reared in *P. kenyae*. Some of the predators were reared and liberated but are not thought to have become established. A few of the small encytrid *Pauridia peregrina*, parasitic on *P. krauhniae*, were received alive from Honolulu. They were not reared, but several years later the same species, parasitic in this case on *P. kenyae*, was received from Uganda and appears now to be satisfactorily established in Kenya.

A few further efforts to use enemies of various mealy-bug species were made, notably the introduction of *Leptomastix dactylopii*, made through the kindness of the University of California's Citrus Experiment Station, which had previously introduced the parasite to California from South America, and with the help of the Imperial Institute of Entomology, from whose laboratory at Farnham Royal we received some excellent shipments of this parasite of *Pseudococcus citri*. Large numbers of the parasite were available for experimentation, but though they would often oviposit in *P. kenyae*, only two male specimens were reared from many thousands of *P. kenyae* exposed to the parasite. This introduction was, therefore, also unsuccessful.

Introduction of parasites from Uganda.—The crucial importance of correct specific identification of an insect is nowhere more evident than in this case, where numerous unsuccessful attempts at biological control were made, involving the tapping of beneficial insect resources in four continents, when a large number of valuable primary parasites were present all the time in a neighbouring country. As soon as the insect was recognized to be quie distinct from *P. lilacinus* it seemed likely that it would prove indigenous in some part of its African range outside Kenya.

On the writer's return from the Orient in 1937, staff was available for a search for parasites in Uganda and neighbouring territories, which was begun early in 1938. In this case the exploration and collection was done by A. R. Melville, whilst the receiving end in Nairobi was in charge of the writer. Some primary parasites were early obtained and sent to Nairobi with further species of which the biology was not known. Some of these were primary parasites, and a large number hyperparasites. From the large number of collections of mealy-bug material sent, 9 species were proved to be primary parasites and were reared on *P. kenyae* in the quarantine insectary in Nairobi, the hyperparasites being destroyed. The work rapidly increased in Nairobi, as it entailed not only the biological studies mentioned but also the production of stocks of the primary parasites for liberation.

At this early stage the question whether to make introductions of all the available primary parasites at once, or to concentrate on one or two species only, had to be decided. The former alternative was accepted, as it took into account the urgency of the problem, which required that if there were any outstanding parasite, its economic effect should operate from the beginning of the project. At the same time, it was realized that this might make it more difficult to establish less important parasites later; though if the mealy-bug population were reduced so low that other parasites could not be established, they would hardly be required, and the parasite which could operate at the lowest host density would be the most effective. Although, theoretically, information might sometimes be gained by introducing one parasite at a time and studying its effect separately, this plan is not justifiable in cases of economic urgency. In the present case if one parasite at a time had been used, the first selected would doubtless have been the unnamed *Anagyrus*, because it was the most active and efficient breeder in the laboratory, the second would probably have been *Leptomastix*, after that *Pauridia*, and then perhaps a *Tetracnemus* or *Coccophagus*. The *Anagyrus* near *kivuensis* is unlikely to have been tried early because it is almost, or perhaps quite, indistinguishable morphologically from a species of *Anagyrus* near *aurantifrons* which was already present in Kenya, occasionally parasitic on *P. kenyae*, but of no economic value. On such a plan, therefore, it might have been many years before the most valuable parasite was employed and the project would, during all that time, have been a comparative failure. As it was, the economic effect of *Anagyrus* near *kivuensis* began to operate from the beginning and was having a decided effect on mealy-bug populations early in 1939. Further, despite the dominance of this *Anagyrus*, it has been found possible to establish two other species, the other *Anagyrus* and *Pauridia*. It was found possible to use 5 of the 9 species of parasites and maintain these in constant production, and the project since that time has entailed the multiplication and liberation of large numbers of these 5 species throughout the infested area in Kenya. The remaining 4 parasites, 2 species of *Anagyrus*, 1 *Tetracnemus*, and 1 *Coccophagus*, could not, with the facilities available, be simultaneously brought into mass production, but they are available in Uganda for use at a later date, if necessary, and it is almost certain that some other primary parasites, perhaps a considerable number, remain to be discovered. It is unlikely that any of these is of much importance in Uganda, as the exploration and collecting work was very thoroughly done, but any one of them might prove of more importance when introduced to Kenya. The possibilities of further exploitation of the controlling complex in Uganda are by no means exhausted.

Position in Kenya before the parasite introductions from Uganda.—In the European areas the only major crop affected is coffee, the damage done to other plants being almost confined to gardens, where such plants as passion-fruit and various ornamentals are attacked. However, from 1923 the insect has been not only a major pest of coffee but one of the notable mealy-bug plagues of the world. From 1923 to 1930 all

kinds of control measures were tried, some of them in desperation; these included spraying with many chemicals, collection and dissemination of indigenous coccinellid beetles, various soil treatments, and banding by many methods and with many substances. One of these substances 'Kresotow', a coal-tar oil of high boiling-point, promised to be effective in preventing access of the mealy-bug ant to the trees, with the result that when this was done, the predacious insects present would eventually reduce the mealy-bug population, though considerable crop losses always occurred before this final result. Kresotow-banding soon became fairly general and from 1927 to 1929 nearly 15,000 gallons were imported (*Dept. Agric. Kenya Ann. Rept.* 1929). Then difficulties arose in obtaining a standardized product: it was a by-product of coal-tar distillation, and so varied according to the coal used. Various oils imported for this banding penetrated the grease-proof paper bands and damaged the trees. This induced a search for other methods of banding, and after some time the use of tree-banding greases applied direct to the bark of the trees became general. The loss of crop in the first few years of mealy-bug attack, before the development of Kresotow-banding, was prodigious,[1] and even after it the loss of crop, before the predators got the upper hand, was usually considerable. The loss in the period 1923–30 before the use of grease-banding may be conservatively estimated at 10 per cent. of the crop in the mealy-bug area. The grease-banding was a great improvement, but it was costly, for by that time the pest had become so severe and general that year-round banding was necessary. From information supplied by six out of the seven or eight firms which sold banding-grease in the country, it is known that a total of more than 1,300 tons of tree-banding grease was imported from 1932 to 1939. This represents an expenditure on grease and labour for applying it of approximately £33,000 a year. The grease-banding, however, was fairly effective. By means of year-round and extremely careful banding some planters considerably reduced the loss of crop through mealy bug; but any relaxation of the constant supervision entailed in seeing that the bands were frequently refreshed, and any delay in removing weeds which touched the trees, was likely to result in a severe attack, and many such occurred with great loss of crop. Probably the crop loss over the mealy-bug area during this period was about 5 per cent.

The following is an estimate of the cost of mealy bug on coffee in the period 1923–39:

	Total £
Expenditure on control 1923–30, £16,500 per annum . .	132,000
Expenditure on control 1931–9, £33,000 per annum . .	297,000
Value of crop lost 1923–30, 10 per cent. loss	377,000*
Value of crop lost 1931–9, 5 per cent. loss	286,000*
Total	£1,092,000

* Calculated from data in Kenya Dept. Agric. Ann. Repts.; Kenya Agric. Census; Kenya and Uganda Ann. Trade Repts.

[1] Kirkpatrick (The Common Coffee Mealy Bug, Nairobi, 1927) estimated a loss of £100,000 in the first six months of 1927.

This amounts to about £64,000 a year for 17 years, and in addition there are the costs of direct expenditure by Government on research services throughout the period, and by the Colonial Development Fund on journeys for parasites. No attempt will be made to assess the total expenditure under these heads, but the Departmental Report for 1929 states that some £9,000 was sanctioned by Government for building, equipping, and managing insectaries for the breeding of predatory ladybirds. It seems probable, therefore, that the cost of mealy bug on coffee up to 1939 had been between £1,000,000 and £1,500,000.

The loss from destruction of crop plants in the native areas cannot be estimated with any approach to accuracy. The damage done is to yams, pigeon peas, beans, potatoes, and some other food-plants, to cotton and to many indigenous herbs and to certain useful shrubs and trees. In some areas the cultivation of yams ceased completely following severe and persistent mealy-bug attacks, and agricultural cropping practices of long standing, such as the ratooning of pigeon peas, had to be modified. The damage to native agriculture has made a marked difference to the prosperity of thousands of small landowners over a wide area, and the aggregate annual loss must have run into many thousands of pounds.

Liberation of mealy-bug parasites.—The first liberations were made in 1938 while parasites were being actively sought in Uganda, and the first undoubted result was seen 6–8 months afterwards, when a heavy attack of mealy bug was completely suppressed by one of the parasites. Every year since then a large number of parasites have been liberated, and by 1940 mealy-bug populations had decreased over a wide area.

The five species of parasites used are not all identified or named, but they belong to four different genera, and are referred to by the following names:

Anagyrus sp. near *kivuensis* Compere; *Anagyrus* sp.; *Pauridia peregrina* Timberlake; *Leptomastix bifasciatus* Compere; and *Pseudaphycus* sp.

Of these insects the first has proved outstanding; it possesses all the chief attributes of an efficient parasite: it is vigorous, hardy, adaptable, mates readily, and is an excellent searcher. It appears capable of maintaining itself on a very low and scattered mealy-bug infestation, because, since 1940, with hardly any exception, every sample of mealy bug taken from coffee, or from other plants in the native areas, even in cases of extremely slight attack, has produced a number of this species of parasite. This insect alone, without help of banding, has completely controlled infestations in districts where for 10 or 15 years it had been necessary to band large areas at great expense.

The other *Anagyrus*, yet unnamed, is an extraordinarily vigorous breeder. The present stock was begun with three virgin females that were found in a shipment of other insects; they were immediately used to produce some males parthenogenetically, and it proved possible to keep two of the females alive until some males emerged. From the union of these insects the stock was developed. This insect is extremely easy to breed in the laboratory and larger numbers can be produced, with

equivalent labour, than of any of the other parasites. For some time recoveries were few, and the parasite has not shown the numerical dominance in the mealy-bug infestations exhibited by *A.* near *kivuenis*, but it has been spreading rapidly, is now taken in about half the samples examined, and on occasions is very numerous and of distinct importance.

The other parasite which can probably be considered established is *Pauridia peregrina*. This was first liberated early in 1939 and was not seen again (except the recoveries from the mealy bugs present when the liberations were made) until 1941, when it was recovered in large numbers very near the original site. A detailed search of neighbouring places proved that it had already spread some distance. This insect has been recovered from several widely separate localities in coffee districts and native areas, but is not yet generally spread. It is thought unlikely to become a major factor in the control of the mealy bug, but since it is a small insect attacking small mealy bugs, it may well prove a valuable addition to the introduced fauna.

The other two species have not yet become established. *Leptomastix* appeared to do well at some sites, successfully passed at least 20 generations in the field, and spread some distance from the original liberation site, but later examinations in these areas have not confirmed its establishment. It may be that this insect will eventually prove to have persisted, but it does not at present seem likely to be of much use. *Pseudaphycus*, of which several, up to eight, develop in one mealy bug, and of which there are normally three times as many females as males, might well prove a very useful addition to the list of parasites, has not been recovered except directly after liberation. It is possible that this insect may become established later, probably at the lower altitudes, but from its behaviour up to the present is unlikely to become important.

The liberation programme was carried on as actively as possible in European and native districts. From September to December 1938, about 15,000 parasites were liberated. From 1939 to 1941 about 200,000 parasites were liberated each year, and the whole of the mealy-bug area was covered.

Position in Kenya after the establishment of the introduced parasites.—What economic effect have the parasites had up to the present, and what are they likely to have in the future? Both these questions are extremely hard to answer; it is always difficult to confirm that a favourable economic result is in fact a result of parasite introductions and not a short-term change in the incidence of the pest. This is confirmed with certainty only if over a long period the population of the pest is markedly reduced, and such certainty is not available in this case where the first establishment was confirmed less than three years ago. However, to anyone who has worked in the mealy-bug area, whether as an entomologist or planter, the difference in respect of mealy-bug attack now and before is so obvious, and so clearly follows the establishment of parasites, that there is no doubt that in these first years the parasites have had a marked effect on the intensity of the infestation, and some of the evidence that this is in fact the case will be given.

A short questionnaire was recently sent to planters asking for such

records as were available on the cost of mealy-bug control on their plantations for the past 10 years. These plantations were not specially selected except in so far as (*a*) they were all in the mealy-bug area, (*b*) they were known to be under the same management as before the war. This point is important because despite the war there was a continuity of policy regarding the use of banding when necessary, and without exception the farms listed are believed to have been run as efficiently after the war began as before. There was no shortage of banding-grease, in fact large stocks were held by suppliers, and many planters had stocks on the farms. Twenty planters gave detailed figures of the cost of mealy-bug control and these are set out in the table. In addition, replies were received, without detailed figures, covering 12 other plantations. The area of coffee covered by these returns was approximately 10,000 acres, or about one-sixth of the total coffee acreage infested. Of the 32 plantations, 28 recorded a definite decrease of mealy bug in the last two years; 1 records mealy bug as severe as before, and the remaining 3 are doubtful. On 10 of the above 32 plantations where regular banding was necessary before the establishment of parasites, banding was completely dispensed with afterwards. The following notes are required in explanation of the results given in the table. The column headed 'First proof of establishment of *Anagyrus* sp. near *kivuensis*' gives dates taken from records of parasite recoveries. The actual date of establishment may, in any particular case, be earlier than that recorded. It may even be earlier than the date of first liberation, which is seen in No. 8, as this occurs through natural spread of parasites before liberations were made on the estate in question. In the table a dash (—) in any column indicates that data in respect of that year were not given, a nought (0) indicates that there was no expenditure on mealy-bug control for that year. Explanations of the series of noughts on plantations 2 and 7 of the table are given in the notes following the table.

Planters' notes (*numbers correspond with numbers in column 2 of table*)

2. 'Ceased routine banding June 1940.'
4. 'Since the liberation of parasites mealy bug has almost completely disappeared.'
8. 'In July 1940, due to the apparent success of control of the mealy bug by the introduced parasite, a chance was taken and all grease-banding was stopped. Since that date no banding has been done. The results to date have justified the decision to stop banding. During 1941 nothing was spent on control. The natural control, if it continues, will undoubtedly mean increased average yields of coffee. This district was considered one of the worst mealy-bug areas.'
10. 'Two tons banding-grease purchased Sept. 1939, used two or three drums only, mealy bug appears to be completely under parasitic control.'
11. 'No coffee banded for the last two years, before that 150 acres were kept banded.'
12. 'From 1934 to 1939 all acreage banded; 1940 only scattered trees banded, no banding done in 1941. No need for it, mealy bug in complete control by parasites.'

Cost of Mealy-bug Control on Twenty Farms in Kenya, 1930–9

District	*No.*	*Annual cost in £'s before parasites were established*										*First liberation of* A. kivuensis	*First proof of establishment of* A. kivuensis	*Annual cost in £'s after parasites were widely established*	
		1930	*1931*	*1932*	*1933*	*1934*	*1935*	*1936*	*1937*	*1938*	*1939*			*1940*	*1941*
Kiambu	1	—	53	229	198	101	107	42	70	88	67	None	Not known	11	8
,,	2	0	0	0	0	34	93	395	199	240	253	June '38	May '40	76	34
,,	3	120	100	90	150	4	90	82	128	40	80	June '39	Dec. '39	50	0
,,	4	—	308	306	405	200	146	566	202	74	33	Dec. '40	May '41	25	0
,,	5	—	133	192	127	94	137	221	193	163	240	Aug. '40	Aug. '40	46	0
,,	6	160	215	124	81	93	77	100	226	165	45	Oct. '38	Dec. '39	22	18
,,	7	0	0	0	0	10	35	107	143	77	82	Dec. '39	Feb. '40	20	15
Ruiru	8	—	1,210	1,116	842	446	474	364	598	608	1,520	July '41	Jan. '40	454	0
,,	9	350	750	457	468	815	625	927	603	670	832	June '39	Sept. '40	179	262
,,	10	—	—	292	—	256	398	587	653	630	680	Nov. '40	Nov. '40	20	10
,,	11	130	242	568	274	172	240	188	178	82	280	None	Not known	182	0
,,	12	—	—	—	—	86	90	168	108	120	214	July '40	Aug. '40	44	0
,,	13	—	—	—	—	—	—	501	472	366	453	April '39	Nov. '39	140	0
,,	14	—	—	—	163	141	114	177	133	157	169	Dec. '41	Dec. '41	66	51
Thika	15	—	—	480	95	118	162	185	198	237	272	Nov. '39	Aug. '40	38	0
Makuyu	16	599	517	385	403	490	465	428	380	347	205	July '40	Aug. '40	167	63
,,	17	—	360	395	252	193	216	323	224	375	210	Aug. '39	Mar. '40	25	5
,,	18	—	—	—	—	79	70	104	45	108	78	Jan. '40	Not known	0	0
D. Sabuk	19	160	376	358	425	344	165	484	425	538	387	Nov. '38	Sept. '39	0	0
Machakos	20	—	—	—	50	8	28	6	34	112	152	Feb. '40	Dec. '40	66	20
Mean annual cost per farm reporting		190	328	333	246	194	196	298	260	255	313	..	..	82	24

16. 'Since parasites were released very little banding has been required.'
17. 'Almost impossible to establish young coffee (re-fills) before the introduction of parasites.'
19. 'Last two years no banding, before this an average of 300 acres banded per annum.'

The following are notes made by planters in respect of plantations for which detailed figures were not provided:

(*a*) 'No grease has been used since September 1939.'

(*b*) '99 acres banded completely and always, but after receiving parasites in 1939 there was no need for further banding until Dec. 1941, when a few isolated trees were banded. Expenditure on mealy-bug control: 1936, £81; 1937, £92; 1938, £40; 1939, nil; 1940, nil; 1941, £1.'

(*c*) '263 acres practically all banded from 1930 to 1939, i.e. for ten years. In 1939 we laid in a large stock of banding-grease which lies unused.'

I add my own comments under the relevant numbers:

1. Establishment here by natural spread probably about 1940.
2. Mealy bug not serious here before 1934, as the area was free from *Pheidole punctulata*, the mealy-bug ant. This arrived, or was accidentally introduced, about 1933, and thereafter mealy bug much increased in severity. [In 1931 I recorded an area in which this estate is situated as free from *P. punctulata* and stated 'it appears almost certain that these areas will eventually become infested'.[1]]
7. This plantation was also free from *Pheidole punctulata* until about 1933; mealy bug was present but never serious until the ant appeared.
8. A striking case, 1,100 acres of coffee in worst mealy-bug area—able to dispense entirely with banding for first time in more than 10 years.
9. Fairly severe attack persisted here despite early spread of parasites to the coffee.
14. A marked result, *Pauridia peregrina* as well as *Anagyrus* near *kivuensis* established (by natural spread) here.
17. A very striking result, constant complete banding previously essential, after establishment (which took time) no appreciable mealy bug remained and large numbers of parasites are regularly recovered in all samples.
19. A plantation in a warm district where extremely severe mealy-bug attack has previously entailed constant banding; now no banding is necessary, mealy bug is usually difficult to find and when found is always heavily parasitized; very large recoveries of parasites are always made here. This plantation adjoins that of note (*c*) above, and the same conditions are now found on both.
20. A district in which parasites were expected to do well, but where in fact they proved to be very difficult to establish. Establishment was, however, finally attained, and the mealy bug seems to be decreasing now.

The one estate previously mentioned on which mealy bug did not decrease during 1940–1 requires mention. Despite natural spread of *Anagyrus* near *kivuensis* to this estate some time in 1939, the parasite did not increase and mealy bug remained severe almost throughout 1941, though it began to clear just before the end of the year; no reason was obvious for this severe infestation, and other estates near by cleared up satisfactorily.

[1] *J. East Africa and Uganda Nat. Hist. Soc.*, 1931, Nos. 40 & 41, 67.

The establishment of the parasites (especially *A. kivuensis*) had a remarkable and extremely rapid influence on the population of mealy bug, the decrease occurring with almost incredible speed and to an almost unbelievable extent on many farms, and similarly in many places in the native reserves. This decrease in the native reserves is difficult to demonstrate; it may perhaps best be suggested by a comparison of the condition bordering the main motor-road from Embu to Meru in 1938 and later in 1941. In 1938 a motorist would notice frequent areas near the roadside where the trees, bush, and weeds were black: areas which stank of mealy bug, the severity of the attack being unmistakable and the areas very obvious from a moving car. The liberation in 1939 in this area was easy, one motored to a severely attacked patch, liberated parasites, and then on for a mile or perhaps 2 or 3 miles to another. In 1941 near the main road there were no such areas. A detailed search was necessary in order to find any mealy bug at all, and severely attacked areas at a distance from the road had to be located in advance by African employees of the Agricultural Department and visited on foot. By the end of 1941 even these were seldom reported. At Meru where the mealy bug arrived only in 1939, the parasites were liberated almost immediately and the mealy bug was actually controlled before it had had time to do any serious damage. Natives in the area knew it for a short while in a few scattered but fairly severe attacks, and then very soon after had great difficulty in finding enough of it to warrant further parasite liberations.

The extremely rapid decrease in the European coffee areas is more easily demonstrated; it is reflected in the table, where the columns referring to 1940 and 1941 show a very marked general decrease in expenditure on mealy-bug control. This is also shown in the records of banding-grease sales. Instead of an average of 165 tons per year, six leading suppliers sold approximately 77 tons in 1940 and 33 tons in 1941. The loss of crop through mealy bug was small during 1940 and 1941, although only a few estates had considerable losses. An average loss of 2 per cent. of the crop in 1940 and 1 per cent. in 1941 over the mealy-bug area is not thought to be an underestimate of the loss through mealy bug. This would represent a loss of about £11,000 for the two years. The saving during these two years, on the previous average annual cost of mealy bug through decreased banding (but allowing for a 50 per cent. increase in banding-grease prices), and through decreased loss of crop, would work out at approximately £24,000 in 1940 and £43,000 in 1941. It is thought that these estimates are conservative.

How far may we expect this remarkable decrease in mealy-bug population to be maintained? Probably it will not be maintained with the same completeness. The first effect was a rapid breeding up of the parasites almost without check, which resulted in the completeness of the 'clean-up' observed; later, local influences may be expected to come into action which will reduce the efficacy of the parasites. The chief of such local influences will be hyperparasites, and already there is evidence that local polyphagous hypers have appeared here and there in large numbers. It is customary to-day to minimize the importance of hyper-

parasites, because so many parasites are able, despite the hypers, to maintain sufficient numbers to control the pest, but there seems little doubt that the rich continental fauna of Kenya will produce damaging hypers, and that these will have a damping effect on the primaries. It seems probable that the primary parasites already introduced will leave the position, though much ameliorated, still sufficiently serious to entail regularly a certain amount of banding, and still sufficiently unstable to allow fairly severe, perhaps widespread, attacks to develop at intervals. Decisions on whether to attempt the introduction of further parasites to supplement the controlling complex already introduced will have to be taken when the position has become more stable, and when long-term results of the project are available for study.

Summary

1. *Pseudococcus kenyae* is a mealy bug comparatively recently introduced to Kenya, where it rapidly became a major pest of coffee and of some native food crops.

2. Attempts to introduce controlling parasites and predators from various hosts proved unsuccessful.

3. Following the determination that the insect was an undescribed species, known only from East Africa, a search for parasites was made in Uganda and Tanganyika, which resulted in the discovery of at least 9 species of primaries, of which 5 were bred in large numbers in Nairobi and liberated in European and native areas.

4. Three of these are now considered to be permanently established and one of them in particular has been of immediate value. The population of mealy bug both on coffee and native crops has decreased with remarkable speed and to a remarkable extent following its establishment. This has appreciably reduced the cost of producing coffee in the mealy-bug area, and has materially assisted many thousands of small producers in the native reserves.

5. This extremely favourable result may not be so completely maintained in future, and though the mealy bug can never be so severe a pest as before the introductions it may still prove to be a pest of some severity. The question of introducing further species will then come up for decision.

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THE GENETIC SYSTEM OF BANANA VARIETIES IN RELATION TO BANANA BREEDING[1]

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Introduction.—A general review of the genus *Musa* and a report of the progress made in the attempt to breed a banana combining the good qualities of Gros Michel with resistance to Panama Disease and Cercospora Leaf Spot have been given by E. E. Cheesman [1]. Later researches confirm the view that the three morphologically distinct groups within the genus are also cytologically distinct and have basic chromosome numbers of nine, ten, and eleven, respectively (Cheesman, unpub.). The cultivated bananas and the wild species (at present not certainly identified taxonomically) from which they originated, all occur within the group with a basic number of eleven, and form a subgroup which is referred to in the present paper as the 'banana complex'. In it, all the wild species and a few edible varieties are diploid ($2x = 22$) but the majority of edible varieties are triploids ($3x = 33$); and experimental hybridization has given tetraploids ($4x = 44$), a few higher polyploids, and some aneuploids.

Essential characters of all bananas classed commercially as 'edible' are a large proportion of edible tissue (or pulp) and the absence of seeds. These characters occur as a result of parthenocarpic development and almost complete female-sterility. Again, the occurrence of female-sterility means that, inevitably, vegetative propagation must be used for the perpetuation of bananas as crop plants. Thus, four factors—vegetative propagation, parthenocarpy, sterility, and polyploidy—dominate the genetics of the banana complex. They have played an extremely important role in the evolution of the edible varieties, and it is the object of this paper to discuss the significance of each, and to develop from a consideration of their interdependence a conception of the genetic system of bananas. Such a concept is of fundamental importance for defining the types of crosses that can be made with a reasonable prospect of obtaining an edible banana, and without it, breeding policy can be no more than trial and error.

The Reproductive System of the Banana Complex

Vegetative propagation.—Though wild banana species reproduce by a sexual process and set seed readily, they all possess the free suckering habit which provides an easy means of vegetative propagation throughout the banana complex. Edible bananas are highly female-sterile and very rarely set seed. Vegetative propagation in them is, therefore, obligatory. The time and manner of origin of the first edible bananas are unknown, but they existed at least five thousand years ago [2]. Present-

[1] This article is published with the full approval of Professor E. E. Cheesman, Head of the Department of Botany of the Imperial College of Tropical Agriculture, to whom the author expresses sincere thanks for many valuable suggestions.

day edible bananas are undoubtedly their vegetative descendants, which have been perpetuated by human agency.

Parthenocarpy.—Parthenocarpy is a developmental behaviour resulting in the formation of a fruit without previous fertilization. Because of it the fruit of a cultivated banana is edible, for the ovary swells, becomes fleshy, and reaches maturity without the formation of seed. Parthenocarpy in the banana can be qualified further and described as 'vegetative parthenocarpy', since the stimulation of pollination is not required. Fruit-formation is not disturbed even if all pollen is excluded from the inflorescence. On the other hand, when pollen is excluded from flowers of wild diploid species the ovaries do not develop but remain immature and eventually shrivel.

From the economic point of view it is important that the parthenocarpic development of the banana fruit shall be accompanied by absence of seed-setting (female-sterility). Although, theoretically, it might be possible for parthenocarpy in the banana to be facultative (i.e. seeds might be set readily although the fruits are capable of parthenocarpic development), this does not appear to be the case. Female-sterility in edible clones is not always complete, but even the least sterile of them show no approach to the abundant seed-setting of fertile, non-parthenocarpic diploids. The most fertile parthenocarpic diploid variety in the Banana Collection at the Imperial College is Pisang Lilan. It produces abundant and viable pollen, but sets seed extremely rarely. No seeds have been obtained on selfing, but a few seeds, of which, however, only two proved viable, have been obtained on pollinating with fertile diploids. Clearly, some factor other than a direct cytological one must be responsible for female-sterility.

The two seedlings, of the parentage Pisang Lilan (♀) × *M. acuminata*, Clone Calcutta 4 (♂), were both parthenocarpic primary triploids,[1] so that diploid gametes from Pisang Lilan must have functioned. In contrast to the behaviour of Pisang Lilan, the only two seedlings from Palembang, another parthenocarpic diploid, were diploids and parthenocarpic. They were of the parentage Palembang (♀) × *M. acuminata*, Clone A of Cheesman and Larter [3]. Although the anthers of Palembang contain very little pollen, those of the hybrids contain abundant pollen. Palembang is a far more complex structural hybrid than Pisang Lilan, and so all kinds of structural arrangements of the chromosomes of Palembang will occur in the female gametes. Evidently in a rare ovule the gametic chromosomes correspond structurally with the chromosomes in the gamete of a fertile diploid. A viable diploid zygote is formed of which the chromosomes pair successfully at male-meiosis with the result that abundant pollen is formed; and even though most structural hybridity is eliminated, the plant has the ability to develop fruits parthenocarpically and acquires the concomitant female-sterility. Although by chance the two plants which have so far been raised from Palembang are diploids, further pollinations might give triploids as a result of behaviour similar to that in Pisang Lilan.

[1] So called to distinguish them from existing triploids and secondary triploids (derived from $4x \times 2x$, &c.).

In the case of the triploid parthenocarpic varieties any differential degree of sterility which may exist between male and female gametes is inevitably obscured by the fact that all triploids, as such, show a high degree of sterility in both male and female gametes. It is obvious, however, that since parthenocarpy and the associated female-sterility occur in diploids, *both these economically important characters must be independent of polyploidy*.

In the collection of banana varieties at the Imperial College there are five parthenocarpic diploid clones. One of these, Pisang Lilan, is genetically simple, apart from being heterozygous for a reciprocal interchange, and, as previously mentioned, it produces abundant pollen. When Pisang Lilan is used as male parent in crosses with fertile diploids abundant seed is obtained. The offspring are parthenocarpic diploids. They are highly sterile on the female side although their anthers contain comparatively large quantities of viable pollen. Since both female-sterility and parthenocarpy have been introduced from the male parent *it is evident that both characters are under genic control*. As they are just as much genetic properties as disease-resistance or fruit-size, their segregation must be considered when deciding the potentialities of hybridization within the genus.

Sterility.—Sterility limited to the female flower and associated with the ability to mature fruits parthenocarpically has been considered above; that due to polyploidy is discussed below under *Polyploidy*. Here other forms of sterility which affect male and female flowers alike are considered.

In the plant kingdom in general, sterility which affects both male and female flowers equally is usually a result of hybridity. When two species are crossed the chromosomes from each parent may not pair regularly at meiosis in the hybrid. Consequently whole chromosomes or parts of chromosomes are lost and the nuclei of the pollen grains and ovules are genetically incomplete. Many inviable gametes occur and seed-yield is reduced. This kind of sterility is prevalent in hybrids between fertile *Musa* diploids, and the quantities of seed set by the F_1 are a measure of the compatibilities of the parents. Furthermore, the sterility of these hybrids is independent of parthenocarpy (unpub. data).

Edible bananas are of extremely ancient origin and they have been vegetatively propagated by human agency for thousands of years. Many are complex structural hybrids. Now the genetical significance of structural changes in the chromosomes of an organism differs according as reproduction is by a sexual or vegetative process. There is an increasing amount of evidence that although structural changes arise most frequently during meiosis, they may occur at any stage of the life-history. In a sexually reproducing organism such structural changes are either rapidly eliminated or else become homozygous in the surviving offspring, and in the latter case, without influencing either vigour or fertility, achieve the first step in their genetic isolation. When, however, reproduction is entirely by vegetative means, structural changes in the chromosomes are not submitted to selective elimination by the sexual process. They therefore accumulate and each new structural change can be

regarded as a further step towards loss of ability for sexual reproduction, inasmuch as each new inversion or interchange interferes with the pairing of homologous chromosomes and reduces the chance of the formation of viable gametes. Indeed, it may be said that the maintenance of a normal sexual process in the face of cytogenetic accidents depends on its continued use. Otherwise the process will in time become impossible and survival will only be by vegetative means.

Stages in the process whereby sterility resulting from structural hybridity has been added to the female-sterility associated with parthenocarpy are still demonstrable within the edible bananas. Of the five sterile parthenocarpic diploids at the Imperial College (Pisang Lilan, Sucrier, Bande, Palembang, and Guindy), only Pisang Lilan forms abundant pollen. Pisang Lilan is a simple reciprocal interchange heterozygote. The others have proved on cytological examination to be complex structural hybrids [4]. It is a fair assumption that they are older clones than Pisang Lilan, which itself might become just as male-sterile after the lapse of a long period of time. Structural hybridity occurs in both diploid and triploid edible bananas. Hence although present-day edible bananas such as Sucrier (diploid) or Gros Michel (triploid) may be identical in external appearance with their original parthenocarpic ancestors, and have exactly the same genes present, these genes have in all probability become quite differently arranged within the chromosomes during the period which has elapsed since the incidence of obligatory vegetative propagation. Moreover, the older the clone, the higher will be the degree of structural hybridity and the lower the ability to set seed.

Polyploidy.—Polyploidy is the presence in an organism of more than two complete sets of homologous chromosomes. Most edible bananas are triploids. Apart from the question of structural hybridity, triploids as numerical hybrids are invariably less fertile than diploids. During gametogenesis in a triploid the chromosomes are distributed irregularly to the daughter nuclei of the pollen mother-cells. Only nuclei containing virtually complete and balanced chromosome sets form viable pollen grains, for extra chromosomes in a nucleus are usually as deleterious to balance, and therefore viability, as are lost chromosomes. Thus, very few of the gametes will contain complete and balanced chromosome sets, and when the triploid is used in a cross the number of seeds will be correspondingly reduced.

Polyploidy is easily induced in bananas, since a large proportion of the functional female gametes formed by parthenocarpic diploid and triploid varieties are unreduced.[1] As seen above, primary triploids can be synthesized by crossing edible diploids with fertile diploids as male parents. However, of the five parthenocarpic diploids only Pisang Lilan and Palembang give offspring when used as female parents. In the others it would appear that parthenocarpy, together with structural hybridity, has led to a loss on the female side of the ability to reproduce sexually.

[1] This natural behaviour is a more efficacious means of obtaining *Musa* polyploids than is an artificial method designed, ultimately, to increase the frequency of polyploid gametes; e.g. colchicine treatment.

Pisang Lilan and Palembang are probably varieties of more recent origin, in the earlier stages of breakdown of the sexual process.

Primary tetraploids can be synthesized by crossing edible triploids with fertile diploids as male parents. Occasionally hexaploid female gametes function, but the resultant heptaploids are slow-growing dwarfs that never flower. Primary tetraploids selfed give secondary tetraploids inferior to the parents and, crossed with fertile diploids, they give secondary triploids that are markedly inferior to the existing edible triploids. Primary tetraploids can be crossed with triploids only by using the former as male parents. The resultant pentaploids are of no commercial promise. The functional female gametes of primary tetraploids are diploid and undoubtedly products of a reduction division. It is not surprising, therefore, that the resulting types show the effect of disintegration of the 'edible' genome. Clearly, *primary tetraploids represent the only step that can be taken in breeding from existing edible triploids without thereafter bringing about a disintegration of the genic constitutions of the existing edible triploids and destroying the results of both natural and human selection.*

Often polyploids show a general increase in the size of their parts. Polyploidy in *Musa* may have played a part in the evolution of the large fruits of the triploid edible varieties, but it must be observed that at the Imperial College there are synthesized polyploids (triploids and pentaploids) derived from wild species, in which the fruits are no larger than those of their diploid parents. For example, when F_1 derivatives of *M. Balbisiana* Colla crossed with other fertile diploids are selfed, or backcrossed using the F_1 plant as the female parent, all the surviving plants are either triploids or pentaploids. These polyploids lack vigour, have no tendency to parthenocarpy, and their fruits are no larger than those of the diploid parents. Experimentally, however, they are of great value as a source of polyploid gametes from fertile varieties. By crossing them with parthenocarpic diploids as the male parents (e.g. Pisang Lilan) it should be possible to obtain many kinds of parthenocarpic polyploids. The value of these types of crosses lies not in their immediate practical application but in their use for determining the mode of inheritance of parthenocarpy in relation to polyploidy, and the factors influencing fruit size.

Experience with *Musa* polyploids suggests that tetraploidy represents the upper limit of vitality in the genus. Pentaploids have elongated leaf bases and loose pseudostems giving a very insecure plant habit. They produce small and irregular fruit bunches. Heptaploids[1] are slow-growing dwarfs which never flower.

Discussion

A possible cause of parthenocarpy.—It appears that a single factor may be the primary cause both of sterility of the female flower and parthenocarpy. Investigations on artificial parthenocarpy produced by chemicals [5, 6, 7, 8, 9, 10] have shown that under experimental conditions auxins

[1] Mr. L. N. H. Larter, Botanist of the Department of Agriculture, Jamaica, informs me that he has obtained a single hexaploid. It, also, is a slow-growing dwarf.

can cause fruit-development without fertilization in plants normally requiring it. Gustafson [6] has proposed the theory that a high auxin-content in the ovary at the flower-bud stage is responsible for natural parthenocarpy. He has shown in a later publication that the auxin-content of ovules and developing seeds is much greater than that of other parts of fruits, and it is considered possible, even though not yet proved, that ovules produce auxin [7]. In the absence of evidence to the contrary it is reasonable to suppose that high auxin-concentrations in parthenocarpic bananas are responsible for their development. And it is perhaps not unduly speculative to associate such high auxin-contents with the female-sterility of parthenocarpic fruits on the one hand, and their marked tendency to produce polyploid gametes on the other. (Polyploid gametes in bananas [4]. Growth-substances and polyploid regions in root-tips of *Allium* [12].) Clearly, there is here a large field of experimental cytology for future investigation.

A breeding programme

(*a*) *Possible methods reviewed: the importance of the male parent.*—A working hypothesis of the probable evolutionary development of the genus *Musa* is indispensable to breeding policy. The analysis given above of the dominant factors involved suggests the following sequence: parthenocarpy and female-sterility arose as gene mutations in fertile diploids and the resultant types with edible fruits were taken into cultivation. Man selected and propagated those producing the fewest seeds and in the course of time parthenocarpy was completely established and vegetative propagation became obligatory. At the same time, as the selective control maintaining the balance of the sexual process was removed, structural changes in the chromosomes of somatic tissues were no longer eliminated and may even have been favoured, as they would further reduce the amount of seed formed. Hence nearly complete male-sterility was gradually added to the existing female-sterility. Stages in this process are demonstrable in the edible diploid varieties at the Imperial College. Finally, at some time in the evolutionary history of the banana varieties, before vegetative propagation became obligatory, polyploidy arose. It is probably the least important event in the series, but triploids may possibly have had larger fruits and therefore been preserved by human selection.

To have any reasonable prospect of success banana-breeding policy must conform to the limitations imposed by this sequence. The present immediate aim is to synthesize a commercially acceptable edible banana which is resistant to Panama Disease and Cercospora Leaf Spot; in effect, to add disease-resistance to the habit (i.e. parthenocarpy, bunch-shape, fruit-size, &c.) and effectively complete sterility of the present commercial banana—Gros Michel. Breeding methods that have been tried or suggested with this object will be reviewed and their value assessed in the light of the above cytogenetic considerations, and an attempt will be made to outline a practical breeding programme.

At the outset it can be asserted that diploid parthenocarpic bananas obtained by experimental hybridization are unlikely to be of direct

economic value. The two necessary conditions of sufficient seed-production for breeding and sufficient structural hybridity to ensure effectively complete female-sterility in the final product are mutually exclusive. Similarly, plants higher than tetraploids are likely to be of no economic value since they are near the upper limit of vitality in the genus. Thus breeding efforts must be confined to the production of either edible triploids or edible tetraploids.

Now to be of commercial value a banana must contain within its constitution the genes responsible for parthenocarpy. Clearly, an edible parent must be used in a cross if edible progeny is desired. However, since edible bananas are structural hybrids, their gene-complexes are disintegrated once they undergo meiosis and the gametes contain all kinds of genic combinations and rearrangements. If, therefore, an edible banana is used as a parent, it is essential that its genome be transmitted intact. Fortunately, the functioning of unreduced eggs when sexual reproduction is imposed on parthenocarpic varieties provides a means of transmitting a complete 'edible' genome. The ploidy of the offspring is, of course, raised at the same time. This limits the possibilities to the fusion of a diploid or triploid, structurally complex, female gamete with a haploid, sexually balanced, male gamete; and new varieties of potential commercial value will be either primary triploids or primary tetraploids.

The edible diploids at the Imperial College all have shorter fruits and fewer hands to a bunch than the existing edible triploids, and these undesirable characters occur in their derived primary triploids. They could not compete successfully with the present commercial bananas. I.C. 2 is a measure of the success that can be obtained by the synthesis of a primary tetraploid. It was obtained by crossing Gros Michel as the female parent with *M. acuminata* Clone B [13].[1] The former, apart from its lack of disease-resistance, is a satisfactory commercial banana, but the seeded diploid male parent has, among other undesirable characters, an almost horizontally borne bunch of small fruits. The undesirable characters of the male parent have had remarkably little effect in I.C. 2. It fails to compete with Gros Michel under existing market conditions chiefly because its fruits are rather shorter than those to which the very conservative trade is accustomed. It will be seen that the possibilities of improvement by hybridization and selection are confined to the sexually-balanced male gamete, *and the opportunity of bridging the gap between I.C. 2 and a commercially successful banana lies in obtaining a fertile diploid which will give better male gametes to unite with the unreduced diploid or triploid female gametes from parthenocarpic varieties.*

(*b*) *The synthesis of a suitable diploid male parent.*—A fertile diploid is required with a gene-complex which, when added to those of edible bananas, will accentuate rather than detract from their desirable characters. It must, at least, be disease-resistant, produce bunches of large fruits which hang vertically, and be sufficiently fertile to breed and remain diploid so that a pure line can be selected. That a diploid male parent homozygous for bunch-shape, fruit-size, &c., should be used is apparent from the breeding results of Cheesman [1]. He obtained only

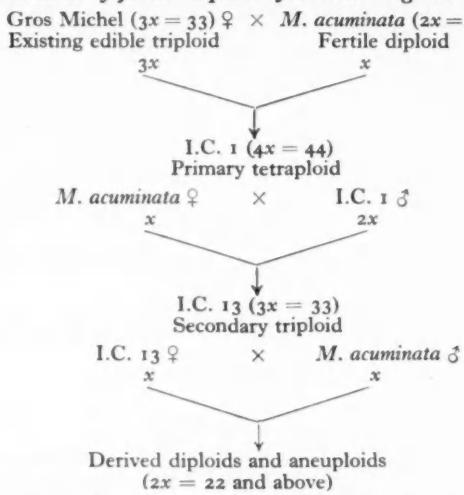
[1] Probable, though assumed, parentage.

14 seedlings from 58 bunches of Gros Michel pollinated with a fertile diploid. Thus, the accumulation of a large number of primary tetraploids of the same parentage would be a matter of great difficulty and best avoided by the use of a homozygous male parent, so that the primary tetraploids need not be selected. There are two ways in which the diploid could be obtained; either (1) by intensive exploration at the centres of origin of *Musa* varieties, or (2) by experimental hybridization. Both methods must be tried, but in the present world conditions the latter is the only one available. Therefore the genetics of the fertile diploids is of fundamental importance to the immediate banana-breeding problem, and a breeding programme must be devoted to them in order to determine the genetics of disease-resistance, bunch-shape and habit, fruit-size, &c., and the extent to which a better diploid can be selected.

The fertile diploids at present available at the Imperial College are mostly varieties of *M. acuminata* Colla, *M. Banksii* Von Muell, *M. Basjoo* Sieb., and *M. Balbisiana* Colla. All, with the one exception of *M. Banksii*, Clone Samoa, have small fruits, and most have, in addition, asymmetrical and nearly horizontal bunches. They give uniform progenies when selfed, so the undesirable commercial characters must be homozygous. On intercrossing, the F_1 derivatives are diploids of intermediate appearances and with different degrees of fertility obviously depending upon the parental compatibilities. No amount of breeding and selection will remove their undesirable characters and substitute good ones. The responsible genes will exert their deleterious effects when added to the gene-complexes of the existing edible bananas. It can be stated with confidence, therefore, that an entirely suitable seeded diploid is not likely to be synthesized by hybridization and selection among these seeded diploids. *M. Banksii*, Clone Samoa, has larger fruits than the other seeded diploids, though its fruits are not as large as those of the edible bananas. It is a weakly clone which does not thrive under Trinidad conditions. Nevertheless, by crossing it with *M. acuminata*, Clone Tavoy, which, in addition to being disease-resistant and vigorous, produces a larger vertical bunch of small fruits, it should be possible to select a hybrid usable as an acceptable male parent in the synthesis of a commercially desirable primary tetraploid.

The only other available large-fruited bananas are edible. However, it has been seen that the selfing of a primary tetraploid brings about a disintegration of the gene-complex of the constituent edible triploid. By continued back-crossing of a primary tetraploid to a seeded diploid, it should be possible to obtain functional haploid gametes derived from the former and to eliminate parthenocarpy in the resultant diploids. Among such diploids, some should combine genes for large fruit-size from the triploid with those for disease-resistance from the male parent. Crosses which conform to this theoretical scheme have been carried out during the early stages of banana-breeding at this Institution, and are given in the diagram below. They show that parthenocarpy can be eliminated and that diploids with genomes partially those of Gros Michel can be extracted from it. The chromosome numbers of eight of the derived 'diploids' were $2n = 22, 22, 23, 23, 24, 24, 24$, and 31. The genetically

The extraction of fertile diploids from existing edible triploids



unbalanced aneuploids were very feeble plants and the two diploids were weak plants which produced smaller bunches and shorter fruits than *M. acuminata*. The diagram shows that the gametic contribution of I.C. 1 to I.C. 13 is a product of meiosis. Evidently the functional male gamete of I.C. 1 which gave I.C. 13 contained more *acuminata* than Gros Michel genes. Thus by using a secondary triploid which contains a 2x gametic contribution from I.C. 1 composed mostly of Gros Michel genes, derived diploids superior to the available clones of *M. acuminata* might be extracted. Hence the initial step must be to raise large progenies of the parentage *M. acuminata* × I.C. 1, *in order to select the secondary triploid*. It would then be used in subsequent crosses to determine the possibilities of extracting a suitable diploid male parent for the synthesis of primary tetraploids.

Again, the pollen-fertile parthenocarpic diploid Pisang Lilan is undoubtedly most valuable for the synthesis of a suitable diploid male parent. Pisang Lilan is a disease-resistant variety with fruits shorter than those of the existing edible triploids but longer than those of the available fertile diploids. It forms a small and nearly horizontal fruit-bunch. By crossing *M. acuminata*, Clone Tavoy (♀), with Pisang Lilan (♂), it should be possible to produce F_1 diploids which, although parthenocarpic, will be pollen-fertile, and usable as male parents. A true-breeding diploid containing genes for size of fruit equivalent to that of Pisang Lilan, and type of bunch similar to that of Tavoy could then be selected among the progenies of back-crosses of these F_1 diploids to Tavoy as female parent. It will be seen that this synthesis avoids the complexities of inheritance in polyploids.

The writer believes that by concentrating present research efforts on these means of synthesizing a suitable diploid male parent for the pro-

duction of primary tetraploids from Gros Michel, not only will valuable data on the genetics of parthenocarpy, bunch-shape, fruit-size, &c., be obtained, but the breeders' objective—a commercially acceptable and disease-resistant substitute for Gros Michel—is more likely to be attained than by any other method immediately available.

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TAP-ROOT DAMAGE OF COTTON, ASCRIBED TO TERMITES, IN THE SUDAN GEZIRA

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WITH PLATE I

Introduction.—For some years it has been known that cotton plants on both the commercial and the experimental areas of the Gezira Irrigation Scheme[1] were liable to suffer tap-root damage, so that a mature plant would have, instead of a long tapering tap-root, one that ended abruptly, with one or more abnormally thickened laterals.

The extent of this damage became evident when in 1932–3, as a measure to control leaf-curl, the practice of cutting off stems at ground-level was abandoned in favour of pulling up the roots. Earlier, in the absence of direct observation, it had been assumed that the tap-root damage resulted from wilt disease. Clouston's [5] work on wilt revealed that to be impossible, since root-damage associated with wilt did not occur in the top 6 in. of soil, the layer where tap-root damage was usually found. Failing wilt, the next most likely agency was termites, and these were known to cause reduction in stand through death of plants, leading at times to bare patches among the crop. The first systematic count of numbers of plants with damaged tap-roots appears to have been made by H. E. King, Senior Plant Breeder, who, in 1936–7, from examination of the breeding-plot at Gezira Research Farm, noted that 'almost every obviously stunted plant examined was found to have a more or less severely contorted, forked, or completely suppressed tap-root'.[2]

A comprehensive series of counts has been made annually since the 1938–9 season, on the permanent and other experiments which have constituted the crop of the Gezira Research Farm. The data collected are shown to be capable of lucid interpretation when studied in the light of a termite hypothesis. The counts did not include plants known to be killed by termites, but were confined to those which, although having sustained injury to their tap-roots, survived through to the end of the season.

Method of observation.—Cotton is sown in the Gezira in August and thinned during September. It reaches maximum leaf dry-weight in late November, and the crop opens ready for picking from late December onwards. The plants are pulled out during late April or May. Unless cropped and therefore irrigated, the land remains dry throughout the year, except during the short rainy season in July and August.

The survey of the tap-roots was made during April and May, immediately after the crop was uprooted. The size of the sample to be observed varied, the aim being to include 5 per cent. of the 'main crop'

[1] For details of the Gezira Scheme see Bluen [1], Lambert [2]; of Gezira soil, see Greene [3], and of crop development, see Crowther [4].

[2] Unpublished note.

cotton of the farm and 10 to 15 per cent. of all plots of all randomized field experiments made during four seasons. This entailed the individual examination of more than 1½ million tap-roots.

Since it is impossible to study the course of damage to the roots of the crop while the plants are yet living in the field, deductions have to be drawn from the damage in its final state, as shown in these end-of-season counts, and viewed in relation to a variety of field conditions which have affected the crop during its early growth.

Nature of the damage.—Healthy plants when pulled out showed a tap-root 25 to 30 cm. long, tapering gradually from 10 to 15 mm. diameter at the collar down to 2 to 3 mm. where broken in the pulling. The tap-root was usually straight, Gezira soil being exceptionally free from stones which might deflect it. There were frequent laterals taking off at right angles from it, usually at intervals of 1 to 2 cm., from immediately below ground-level. Such plants are illustrated in Plate I (Fig. 1, above), but the specimens show the laterals as clinging to the tap-root through damage during extraction.

With damaged plants the tap-root stopped abruptly at 5 to 10 cm. below ground-level. In its place there were one or more laterals greatly thickened and become positively geotropic, having assumed the function of the tap-root. Plants showing typical damage are illustrated in Fig. 1 (below), and in these the laterals are in their true position, since their greater thickness enabled them to resist damage during removal.

Most damaged plants bore no superficial signs of injury, but occasionally specimens were obtained with typical termite lesions. These were also sometimes found on plants with undamaged tap-roots. Such lesions varied greatly in size and number among the plants. They occurred on the thicker laterals as well as on the tap-root. Exceptionally, plants were found in which termites had eaten right into and up the core of the root (Plate 1, Fig. 2). The spaces were filled with soil intrusions, but the injury was not fatal, the plants reaching full maturity.

Damage by termites to living plants, not necessarily resulting in death, is known to occur among many plant species, of which the following are of economic importance: tea in Ceylon [6]; camphor in California, in which a subterranean termite eats into the rootstock, producing a result very like that shown in Fig. 2 [7]; rubber, coffee, cocoa, citrus, sugar-cane, and teak are mentioned both by Light [7] and by Hegh [8]. The last-named authority cites also references to attacks on living avocado, pecan, coconut palms, and many other species of trees, shrubs, and herbs. He even gives (on p. 40) an illustration of Texas cotton-roots damaged by termites, where forking similar to that seen in Fig. 1 is shown; but he states, however, that these particular roots were also infected with root-rot.

Distribution of the Damage in Relation to Season and to Experimental Treatment

The four years' counts made at Gezira Research Farm gave the following percentages of damaged plants:

TABLE 1. *Mean Tap-root Damage over Whole Crop*

Season	*Percentage of crop with damaged tap-roots*
1938–9	32·6
1939–40	34·7
1940–1	30·7
1941–2	27·3
Average	31·3

About one-third of the crop is damaged each year and the percentage shows little variation from year to year.

In analysing the individual experiments, where descriptions and yields of the particular experiments have been published in detail, references only are given. Of the remaining experiments brief notes and yields will be found in annual reports of the Agricultural Section [9]. Whenever possible the average of data for all the years is given, and, in addition, the significance of treatment differences by the z test for the individual years.

Crop rotation.—Cotton at Gezira Research Farm is grown on the same land once in three years and the results from various three-course rotations, different combinations of dura (*Sorghum vulgare*), lubia (*Dolichos lablab*), and fallow, are given in Table 2.

TABLE 2. *Tap-root Damage with Three-year Rotations*

(*a*) *Plots 10 to 15*		(*b*) *Plots 105 to 127*	
Rotation	*Percentage damage*	*Rotation*	*Percentage damage*
CFF	30·1	CFF	26·3
CDF	26·8	CLF	27·4
CDD	42·2	CFL	36·1
CLF	28·6	CLL	37·6
CDL	39·7		
S.E. ±0·64		S.E. ±0·68	
Significance[1]		Significance[1]	
1938–9**	1940–1**	1938–9	1940–1**
1939–40	1941–2**	1939–40*	1941–2**

The experiment in Table 2 (*a*) has been in progress for 16, and that in Table 2 (*b*) for 7, seasons.

Both experiments showed a striking *increase in tap-root damage in those rotations which were cropped the year before cotton.* The difference was consistent from year to year, and reached significance in 3 out of 4 years. This result constitutes one of the strongest pieces of evidence for linking tap-root damage with termites; for cropping with dura or lubia, by providing additional food material, would naturally lead to an

[1] The asterisks in this and subsequent tables refer to significance by the z tests. Those with one are significant at the 5 per cent., and with two at the 1 per cent., level.

increase in termite activity, which, in turn, would mean attacks on the following cotton crop more severe than in those rotations where a fallow of at least 12 months' duration intervened.

Results from an experiment comparing rotations of different durations which has been in progress 11 years, are summarized in Table 3.

TABLE 3. *Tap-Root Damage with One- to Four-year Rotations*

Rotations where fallow preceded cotton		*Rotations where lubia or dura preceded cotton*	
Rotation	*Percentage damage*	*Rotation*	*Percentage damage*
CF	26·6	CD/L[1]	40·1
CFF	26·8	CFD/L[1]	39·5
CD/LF[1]	29·9		
CFFF	27·5	CFFD/L[1]	34·9
CD/LFF[1]	32·6		
CFD/LF[1]	30·6		
S.E. ±0·79			
Significance	1938–9** 1939–40		1940–1** 1941–2**

Mean Percentage Damage over All Rotations

Previous crop	*Percentage damage*
Cotton . . .	32·7
Dura . . .	37·2
Lubia . . .	39·3
Fallow . . .	28·3

These rotations again showed increased damage where dura or lubia immediately preceded cotton. There was also an indication, not attaining significance, that dura or lubia, *wherever its place in the rotation*, led to more tap-root damage than fallow. Generally, lubia is associated with a slightly higher percentage damage than dura.

The position of continuous cotton appears at first sight anomalous, for damage there was less than would be expected from annual cropping. But cotton roots are not concentrated in the upper soil to the same degree as are those of dura and lubia. Moreover, the larger roots of cotton are pulled out and burnt after harvest, whereas dura and lubia crops are cut off at ground-level and the whole root-system is left behind. This contrast will be referred to in the discussion, for it has been noted also in counts of *deaths* of plants from termites.

Manuring.—Green manures led to increased tap-root damage, and there is some indication that cotton cake operated in the same way (Table 4(*a*)).

The lubia in all cases was buried 18 months before cotton-sowing, the rotation of crops being cotton-lubia-fallow. In the rotation experiments described earlier, the lubia was either cut and removed or grazed.

[1] Lubia and dura alternating in successive cycles.

TABLE 4. *Tap-root Damage with Organic Manures*

(*a*) *Green manure and cotton cake* (*Plots 84 to 131*)		(*b*) *Compost* (*Plot 37*)	
Treatment	*Percentage damage*	*Treatment*	*Percentage damage*
Lubia sown July, ploughed-in Oct.	22·0	*Expt. 1*	
Lubia sown July, ploughed-in Nov.	28·2	Unmanured	29·2
Lubia sown July, ploughed-in Dec.	33·7	Compost (40 r.N.p.f.)[1]	24·9
		S.E. ±1·57	
		Expt. 2	
Control—no lubia	18·1	Unmanured	43·5
Cotton cake applied 3 months before sowing	22·2	Compost (20 r.N.p.f.)	31·2
		Compost (40 r.N.p.f.)	31·8
S.E. ±0·45		S.E. ±2·16**	
Significance 1939–40 1940–1** 1941–2**			

Thus lubia grown 2 years before cotton, and ploughed-in, led to an increase in tap-root damage similar to that with lubia grown 1 year before cotton, and grazed. On the hypothesis of termite activity, green manure provided more food for termites than grazed lubia and so maintained them for a longer period. The longer the lubia grew, the larger the crop, and the greater the subsequent tap-root damage to following cotton.

The increased damage from cotton cake was slight, but significant, and was of the same order in each of the three seasons. Although of small bulk as compared to a lubia crop, the amount of cotton cake appears to have been sufficient to attract termites. Confirmation of this attraction is provided by direct observation on an experiment (plot 28, 1942–3) comparing (*a*) crushed cotton seed (sieved), (*b*) composted cotton seed, and (*c*) cotton cake, all applied in February to fallow land coming under cotton the following August. The manures were buried by splitting of ridges and, while one set of plots was left dry, another was irrigated at once to facilitate decomposition of the manure. When examined in June the manures on the non-irrigated plots were unchanged. Where the land had been wetted, in all cases they were inextricably mixed up with termite casts.

It is surprising that termites will consume material as rich in nitrogen as cotton cake (6·3 per cent. N), but it is possible that they are attracted by the remains of the seed-coats.

Manuring with compost made in pits, principally from cotton seed, has been tested in two small experiments (Table 4 (*b*)), but, in both, the compost was applied shortly before sowing. The results showed *decreased* damage where compost was applied. This contrast with the other organic manures, quoted above, is readily explained in terms of

[1] r.N.p.f. = rotls nitrogen per feddan; 1 rotl = 0·99 lb.; 1 feddan = 1·038 acres.

termite activity and is, in fact, strong supporting evidence. Organic matter applied many months before sowing is attacked by termites well before the cotton is sown, leaving the termites free to turn to the cotton later, whereas organic matter applied around sowing time diverts the termites from the young cotton plants.

Inorganic nitrogenous fertilizers were without effect on tap-root damage, a result in harmony with the termite explanation. Three separate experiments in each of three years failed to give any significant or consistent difference. The experiments included comparison of types (ammonium sulphate, nitro-chalk, calcium nitrate), amounts, and dates of fertilizer application.

An isolated experiment in 1941–2, involving phosphate, did, however, significantly affect tap-root damage. The 'phosphate' was compared with 'no phosphate' by two methods of application, (*a*) broadcast, and (*b*) below the seed. In the latter method the holes for sowing the seed were made deeper than normal and the superphosphate was deposited in them first, the seed following in the usual way.

TABLE 5. *Tap-root Damage with Phosphatic Manure*

	Percentage damage	
	Broadcast	*With seed*
No phosphate . .	22·8	24·1
Phosphate . . .	19·8	36·5
	S.E. ±0·53**	

In the foregoing experiment termites could not possibly have been responsible for the increase in tap-root damage. But since the increased damage occurred only where the seedlings had to grow through a zone of almost pure superphosphate, the plasmolysing effect of such high concentrations is sufficient explanation. The same effect showed in germination also, more resowing being necessary where superphosphate was applied in the sowing-holes.

Variety of cotton.—The results of 21 experiments spread over 4 years comparing the two varieties (both *G. barbadense*) at present grown commercially in the Gezira are presented in Table 6.

TABLE 6. *Tap-root Damage with Cotton Varieties*

	Percentage damage
Domains Sakel . .	29·3
X1730A . . .	28·8

None of the experiments gave a significant varietal difference and there was no consistent trend from year to year. If explanation of tap-root damage were sought in terms of soil pan or soil texture, this lack of difference would be difficult to explain, for X1730A variety is of more vigorous habit than Sakel; but in terms of termite attack no varietal difference would be expected.

Cultural treatments.—Although present commercial practice allows any weed-growth on fallow land, following the rains, to ripen without interference, other than grazing by animals, recent experiments [10] on the *hoeing* of such fallow have shown striking improvement in yield of the following cotton. The influence of this hoeing on tap-root damage of cotton sown a full year afterwards is shown in Table 7 (*a*).

TABLE 7. *Tap-root Damage with* (*a*) *Fallow Weeding and* (*b*) *Method of Sowing*

(*a*) *Fallow weeding* (*Plots 104*)	*Percentage damage*	(*b*) *Method of sowing* (*Plot 96*)	*Percentage damage*
No hoeing	39·4	1. Sown without pressure in making or closing holes . . .	35·0
Hoed frequently	21·2	2. Normal sowing (light pressure)	39·8
		3. Deeper holes, soil pressed heavily over seeds	31·2
S.E. ±0·88**		S.E. ±2·14	

The data in Table 7 (*a*) suggest that weeds growing on the fallow, in the year before the cotton is sown, resemble a preceding lubia crop in their power to attract termites, whereas, if weed growth is checked by frequent hoeings, termite activity is kept down to a minimum.

Cotton is sown with the native sowing-stick, and as sowing-time coincides with the period of heaviest rainfall there is frequent waterlogging and compacting of the heavy clay soil. An experiment with different methods of sowing (Table 7 (*b*)) failed to show any increase in tap-root damage where the soil was pressed down very heavily on the seed, and thus compacted more than usual. Thus there is no evidence to support an interpretation based on soil texture, for damage would be expected to increase according to the amount of pressure.

Crop *spacing* [11] slightly influenced tap-root damage (Table 8 (*a*)), which gives the average of three years' results).

TABLE 8. *Tap-root Damage with* (*a*) *Spacing and* (*b*) *Thinning Treatments*

(*a*) *Spacing* (*Plots 16–17*)	*Percentage damage*	(*b*) *Thinning*	*Percentage damage*
Close (30 cm.)	20·4	(*a*) Thinned by cutting off tops at ground-level	42·7
Wide (60 cm.)	22·3	(*b*) No thinning	36·4
		(*c*) Thinned by pulling (normal) .	39·2
S.E. ±0·31		S.E. ±2·13	
Significance 1939–40 1941–2 1940–1*			

Wide spacing had a higher percentage of damaged tap-roots than close spacing, but the effect reached significance only in one season. If tap-root damage were caused by unfavourable soil conditions, the more vigorous, wide-spaced plants should be at an advantage, but the reverse proved the case. Assuming termite activity to be the cause, the results suggest a definite seeking out of the plants by termites, for if

tap-roots were encountered only by chance, the damage in the closer spacings would be twice as great, since there are twice as many plants per unit area.

One of the few experiments undertaken specifically for investigation of tap-root damage dealt with *thinning* of cotton (Table 8 (*b*)), for the tap-roots might be damaged during the thinning operation. In the Gezira about 10 seeds are sown per hole and most of the resulting plants are pulled up during September to leave a final stand of 2 plants per hole. Although thinning is therefore a drastic operation, tap-root damage was no greater on plots thinned normally than in those where the same final stand was obtained without disturbing the roots, i.e. by cutting the tops off at ground-level. Thus mechanical damage during the operation of thinning cannot account for tap-root destruction.

Finally, considering *irrigation* experiments, those which deal with water economy in the second half of the growing-season all failed to show differences in tap-root damage. For irrigation at an earlier stage two experiments gave significant results. One of these was concerned with 'pre-watering' the land several months before sowing [12] and the other with waterlogging the land shortly before and after sowing [13]. The results of both experiments are tabulated in Table 9.

TABLE 9. *Tap-root Damage with* (*a*) *Pre-watering and* (*b*) *Waterlogging Treatments*

(*a*) *Pre-watering* (*Plot 8*)

	Percentage damage
(*a*) Normal—no pre-water	48·8
(*b*) Pre-watered heavily end April	68·2
S.E. ±2·94**	

(*b*) *Waterlogging* (*Plot 18*)

	Percentage damage
(*a*) Normal—no waterlogging	35·6
(*b*) Waterlogged 21 days, starting 4 weeks before sowing	35·2
(*c*) Waterlogged 7 days, starting 2 weeks before sowing	39·2
(*d*) Waterlogged 7 days, starting 1 week *after* sowing	58·7
(*e*) Waterlogged 7 days, starting 3 weeks *after* sowing	30·8
S.E. ±2·79**	

Whilst other experiments on pre-watering have given indefinite results, that summarized in Table 9 (*a*) showed a large increase in tap-root damage with heavy pre-watering in April. By contrast with this, similar heavy waterings nearer to the time of sowing were invariably without effect. Waterlogging shortly after sowing caused heavy tap-root damage, whereas 2 weeks later it was without effect.

Evidently pre-watering under certain conditions leads to a marked increase in termite activity, as has been mentioned earlier in connexion with organic manures. What these conditions are is not at present understood, but it is noted that the large difference quoted in Table 9 (*a*) occurred on land where tap-root damage on the control plots was unusually high, suggesting a response to pre-watering where termites are abundant or unusually active. Later, nearer sowing-time, the land

is already wet, since sowing takes place after considerable rain has fallen, and artificial irrigations have little effect once termite activity has been stimulated by the rains.

The increased damage from waterlogging of young cotton plants is an instance where termites are known *not* to be responsible, the cause being peculiar to the abnormal condition produced by the experimental treatment, i.e. root asphyxiation [13]. Cotton, when waterlogged at an early stage of growth, shows acute yellowing of the leaves and stunted stems. On excavation, many of the roots are seen to have been killed, and when waterlogging ceases new roots are rapidly formed near to the soil surface. Under these conditions it is to be expected that tap-roots will suffer. Later, when the plants are older, waterlogging has little effect, for the main roots are below the waterlogged zone. The tops of the plants show little leaf-yellowing and the tap-roots are unaffected.

Effect of tap-root damage on crop yield.—Since it is impossible with plants growing under field conditions deliberately to excise the tap-roots without at the same time interfering with lateral roots or soil conditions, it is impossible directly to compare yields from plots with damaged roots against those from comparable plots with healthy plants. Therefore, large numbers of plants, selected at random each year, were harvested individually and later grouped according to the result of the tap-root examination. The data from three separate seasons are given in Table 10.

TABLE 10. *Yields from Plants with* (*a*) *Damaged and* (*b*) *Healthy Tap-roots*

Season	*Number of plants*	*Yield seed cotton (grams per plant)*	*Loss of Yield*
1939–40 (*a*) Healthy . . .	349	39·9	0·7 grams
(*b*) Damaged . . .	122	39·2	or 2 per cent.
1940–1 (*a*) Healthy . . .	469	44·2	7·7 grams
(*b*) Damaged . . .	109	36·5	or 17 per cent.
1941–2 (*a*) Healthy . . .	452	37·5	4·6 grams
(*b*) Damaged . . .	72	32·9	or 12 per cent.

The plants in all cases were part of crops grown on the standard rotation, cotton following at least one year's fallow. The proportion of damaged roots was therefore never high. The loss of yield was 2 per cent., 17 per cent., and 12 per cent., respectively, for the three successive seasons. By the *t* test the experimental values for 1940–1 and 1941–2 indicate a significance between $P = 0{\cdot}1$ and $P = 0{\cdot}05$.

It may be concluded that loss of yield by tap-root damage is likely to be slight. Whilst there is some evidence to suggest a loss averaging about 10 per cent. for damaged plants over a period of years, this is equivalent to about 3 per cent. for the whole crop, provided tap-root damage continues on its present scale. It must be repeated that any loss of yield through the killing of young plants by termites is additional to this estimate.

Discussion

The evidence favouring the responsibility of termites for most tap-root damage to the cotton crop at Gezira Research Farm may be summarized as follows:

1. The regular increase in damage which occurs when the land instead of remaining fallow is cropped with dura or lubia in the year previous to cotton, or when vegetable matter is present in abundance from any other cause, such as heavy growth of weeds on the fallow.

2. Pre-watering the land several months before sowing, which at times leads to considerable increase in tap-root damage, is known immediately to increase termite activity in the upper soil layers. The numerous termite casts remaining after pre-watered land dries out have already been mentioned. Estimates of termite activity after pre-watering are given below in Table 11. In one case the activity is based upon the number of stumps of dura stubble showing active termites 5 days after pre-watering, whilst, in the other, the activity is expressed as the loss in weight of wooden pegs driven into the soil for a 7-day period.

TABLE 11. *Influence of Pre-watering on Termite Activity (Plot 104, 1942)*

(*a*) *Number of dura stumps attacked*		(*b*) *Loss in weight of wooden pegs*	*gm.*
(*a*) Fallow pre-watered . .	139	(*a*) Lubia, irrigated fortnightly . . .	311·7
(*b*) Fallow not pre-watered . .	38	(*b*) Fallow, irrigated fortnightly . . .	338·2
		(*c*) Pre-watered fallow .	323·0
		(*d*) Dry fallow . .	1·0

The counts are from random samples on a replicated experiment.

The number of dura stumps attacked was increased threefold by irrigation. With wooden pegs, irrigation led to heavy loss, but the loss was negligible in dry soil. Both sets of data were obtained before the main rain-period. With the soaking of the land by heavy rainfall termite activity becomes widespread. Hence further wetting, by heavy irrigations at this time, is without effect on the tap-root damage of the cotton crop sown shortly afterwards.

3. The stage of development of the cotton crop at which tap-root damage occurs is approximately the same as that at which death of plants from termite attack also occurs. This is during August–September, up to the time when the crop is ready for thinning.

The stage when tap-root damage occurs is fixed by two considerations, namely, (*a*) at thinning time already a considerable number of plants show typical damage, as illustrated in Fig. 3, and (*b*) it is clear from Clouston's [5] work on the root system of the cotton plant in the Gezira that severance of the tap-root at a few inches below the soil surface during October or later leads inevitably to the death of the plants, owing to the loss of a large part of the root-system. Only while the earliest formed laterals are still functioning is it possible for the young plants to withstand the drastic interference with the root-system which occurs when the tap-root is excised.

4. The number of plants *killed* by termites varies greatly from season to season, and from plot to plot within any one season. Within a single plot the loss of stand tends to occur in patches. Even so, there is considerable evidence to suggest that, on an average, death of plants by termites is usually greatest where tap-root damage is most severe. The correlation coefficients are given in Table 12 grouped according to direction and significance.

TABLE 12. *Correlation Coefficients of Deaths from Termites with Tap-root Damage, for Individual Experiments*

Season	*Number of experiments, with correlation coefficients*		
	Significantly positive	*Not significant*	*Significantly negative*
1939–40 . . .	3	5	Nil
1940–1 . . .	3	6	Nil
1941–2 . . .	1	3	Nil
Total . . .	7	14	Nil

In two-thirds of the experiments the coefficients failed to reach significance, probably on account of the patchy distribution of deaths, but in the remaining third *all* the significant correlations were positive, death by termites being greatest where tap-root damage was most general.

In 1934–5 the crop on the Gezira Research Farm suffered severe loss of stand from termites, and Mackinnon [14] states: 'The initial stand was in many cases reduced from 100 per cent. mark to under 20 per cent. . . . The infection seems definitely less if a fallow precedes the cotton, but a preceding dura crop seems rather worse than a lubia one'; and 'Termite damage was most severe in the continuously cropped rotations, cotton-dura-dura and cotton-dura-lubia'. Apart from the difference between lubia and dura, the conclusions are identical with those derived from the counts of tap-root damage. Bailey, in an unpublished note, adds the comment 'cotton after cotton does not seem to be badly affected'. This is also the conclusion reached from the tap-root data.

5. There are instances, as mentioned earlier, where plants, although surviving to the end of the season, showed scars typical of termite attack, on tap-root and laterals, as well as soil inclusions within the core of the roots. This activity has been demonstrated by Cowland [15] while trying to kill plants growing in pots by introducing termites into the soil. He remarks: 'Typical field damage [death of plants] was absent, although there were a few cases in which the tap-root and main side-roots had been practically severed, in the termite series.'

6. There are numerous instances, already quoted, from a variety of crops and countries, where similar symptoms of tap-root damage have also been ascribed to termites.

As evidence *against* the invariable responsibility of termites for tap-root damage, two cases are cited in the survey of field experiments. In one of these the roots were injured by being forced to grow through a

high concentration of superphosphate which proved toxic. In the other, damage occurred when young cotton plants were severely waterlogged. In that case the main stem also was stunted and the leaves yellow, and many of the finer roots too were destroyed. In both these examples the conditions were peculiar to the experiment. Superphosphate is not used commercially in the Gezira and no manures are applied in a hole with the seed. Waterlogging to the degree obtained in the experiment occurs only exceptionally under standard practice.

Thus it is concluded that, for the bulk of the crop under general Gezira conditions, tap-root damage is primarily caused by termites.

Termites in the Gezira.—Entomological investigations on termites so far have been concerned only with the death of plants and the resulting loss of stand. Cowland[1] identified two species in the cultivated area, only one of which, apparently, caused the death of cotton plants. The poison bait he used was successful in reducing the numberof plants killed.

Hegh [8] quotes Bequaert as saying that 'La terre d'Afrique n'est, en réalité, qu'une vaste termitière'. With the whole soil a labyrinth of termite channels, it might be considered adequate to postulate that termites attack only living cotton roots when they are obstacles in their path. The spacing results given earlier suggest a deliberate searching-out of the young cotton plants by termites, for the damage, instead of being less with the wider spacings where the roots were fewer in any given volume of soil, was greater than in close spacings. Termites are frequently active among the seed-coats after germination, and with the method of sowing about 10 seeds in a pocket these seed-coats may be responsible for the initial attraction of the termites to the plants. Thus the spacing results may reflect only the searching for the seed-coats. If so, it is impossible from the evidence to decide whether the termites turn deliberately to the tap-roots when the seed-coats have been consumed, or whether they damage them accidentally in their search for other seed-coats.

The dominant role of water-supply in limiting termite activity has been graphically illustrated by Marais [16] from observations made in South Africa. In the Gezira termites exhibit a marked annual cycle of activity in the upper soil layers. Normally during the dry season they are relatively inactive. Artificial irrigations during the dry weather lead to a sudden burst of activity near the soil surface, which dies away as the soil dries out. Likewise during the rains, July to September, the termites are very active, but as the land dries out the activity dies down. In the early part of the rains vegetable matter remaining from previous crops or weeds is devoured first. Later as fresh weeds become widespread they are attacked. Cotton is sown in the middle of the rain-period, and the young seedlings therefore develop during a period of intense termite activity. Good husbandry demands vigorous hoeing of weeds growing among the cotton crop, while they are still small, so that

[1] Harris [17] found that Microtermes spp. attacked cotton in Tanganyika, 'the insects usually entering the plant in the vicinity of the collar, less commonly via the roots'.

they cannot compete with the cotton crop for nitrogen or water-supply, and the results from the compost experiments suggest that, in the absence of adequate food supplies elsewhere, the termites turn increasingly to the young cotton plants themselves.

Deaths in the Gezira from termites are by no means confined to cotton. Pigeon pea (*Cajanus indicus*) is especially susceptible, and weeds, e.g. *Phyllanthus niruri*, are frequently killed. Cereals presumably escape because they possess numerous roots instead of the single tap-root.

Deaths among cotton plants either occur in patches in the field or are sporadic. Tap-root damage is distributed more regularly and therefore appears the more reliable index of termite activity.

Agricultural Implications.—The survey of tap-root damage has not been extended in detail outside Gezira Research Farm, but counts 50 miles north and 30 miles south of the farm showed the damage to be present, but light (Table 13).

TABLE 13. *Tap-root Damage in Gezira Irrigation Scheme (3 Years' Average)*

Gezira observation plots	*Damage per cent.*
Turabi	12·7
Gezira Research Farm .	21·4
Hag Abdulla . . .	14·3

This lesser damage at Turabi and Hag Abdulla is consistent with the rotation differences, for in the past the land has been fallowed for longer periods than at Gezira Research Farm, where the demand for plots for experiments and for fodder for cattle has led to frequent cropping. This increased tap-root damage with closer cropping means that, though at present tap-root damage and loss of stand by termites exercise little influence on crop yields, both will gain in consequence should any closer rotation be introduced. At Gezira Research Farm the peak of influence should have been reached and passed, for until 1934 the land was cropped annually. Then, owing to the severity of termite depredations, the rotation was modified to allow at least 18 months' fallow before cotton-sowing.

Summary

The paper describes the nature and extent of damage to the tap-roots of the cotton crop of permanent and other experiments at the Research Farm of the Sudan Gezira Irrigation Scheme.

From a 4-year survey of the roots when pulled out after harvest it is concluded that the damage is primarily caused by termites. About one-third of the plants comprising the crop at Gezira Research Farm were damaged, and this value varied only slightly from year to year.

Damage was invariably greater on land which was cropped in the year before cotton than on that left fallow. Where weeds were allowed to grow unchecked on this fallow the damage to following cotton was greater than where the fallow was repeatedly hoed. These differences are readily explained in terms of the increased vegetable matter, fur-

nished either by the frequent cropping or by weed-growth, which proved attractive to termites. The same explanation holds for the increased damage which occurred when organic or green manures were applied some time before sowing. By contrast, inorganic nitrogenous fertilizers, which gave at least as large yield increases as organic manures, were without effect on the degree of damage.

It is concluded that the damage almost always takes place during the first 2 months after sowing. Termites are often active among the seed-coats after germination and the damage to tap-roots may arise because the termites, initially attracted to the seed-coats, either move on deliberately to the living roots or damage them accidentally while seeking other seed-coats.

Loss of yield by tap-root damage is likely to be not more than 10 per cent. on the injured plants, or on rotations at present practised, which invariably allow a full year's fallow before cotton, about 3 per cent. on the crop as a whole. With closer rotations increased interference by termites must be expected. In general, the data demonstrate the prevalence and activity of termites under African conditions of agriculture.

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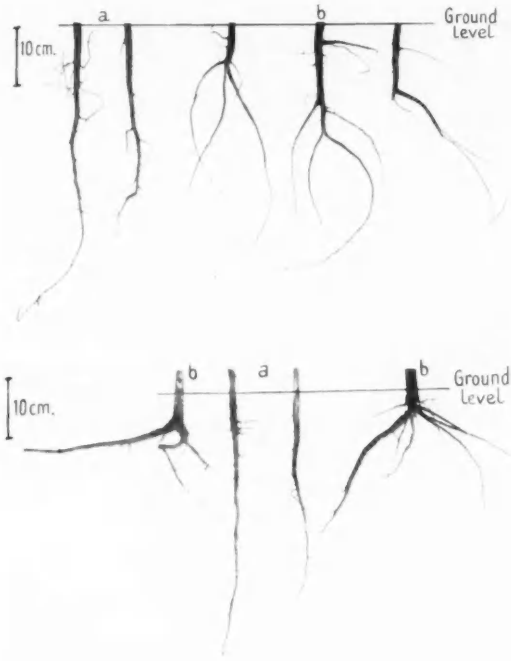

FIG. 1. Cotton roots pulled up at end of season: (above) healthy, (below) damaged roots.

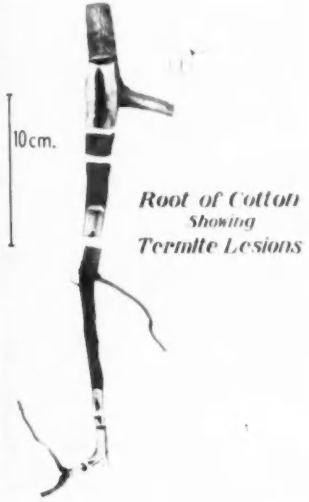

FIG. 2. Root partially cut away to show soil intrusions caused by termites.

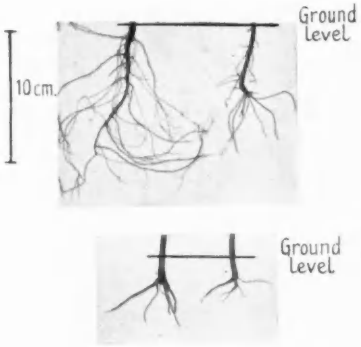

FIG. 3. Damaged roots 4–5 weeks old. Washed out (above), pulled up (below).

EFFECTS OF DEFOLIATION INTENSITY AND FERTILIZER TREATMENT ON TRANSVAAL HIGHVELD

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Introduction.—Much damage has been done and is still being done to South African pastures by overgrazing and overstocking. The gross effects of such practices are well known, manifesting themselves in the dying-off of valuable species of grasses and their replacement by less desirable ones, and in the increase of bare space and subsequent soil erosion [1, 2]. Most soils of the South African Highveld are notoriously low in nitrogen and phosphorus, and consequently respond markedly to fertilizers, which improve both the growth and quality of the herbage, and so render intensive grazing possible [3].

It is, however, very difficult to draw a strict line between intensive grazing and overgrazing since the botanical composition of the sward may also suffer on fertilized and intensively grazed veld [4]. The effects of the grazing animal are multiple and perhaps very complex, but the chief factor involved is probably the degree of defoliation to which the more desirable species of grasses are subjected under different systems of grazing management. The degree of grazing or defoliation intensity to which the veld can be subjected without injury has, however, so far not been ascertained, and, in general, little is known about the interactions between fertilizer treatment and defoliation intensity.

Whilst it must be readily admitted that the effects of clipping and of grazing are in many ways different, much valuable information of fundamental importance can be gained from clipping experiments. The present paper reports the results of a combined fertilizer and clipping experiment which was carried out at Frankenwald, the Botanical Research Station of the University of the Witwatersrand, near Johannesburg, as a contribution towards the study of the above-indicated problems.

Experimental

The soil of the area is a shallow loamy sand on a subsoil of decomposed granite, interspersed with outcrops of laterite (*ouklip*) and quartz. The results of a soil analysis of the fine earth of the surface soil are given in Table 1.

TABLE 1. *Analysis of Surface Soil*

Percentages of dry fine earth

Sand	76·5	Nitrogen	0·102
Silt	14·4	*Phosphoric oxide	0·019
Clay	9·1	*Potash	0·057
		Loss on ignition	3·8
Total colloids	11·6		
Maximum water-retaining capacity	32·8		

* Soluble in 10% HCl.

The soil is decidedly poor in organic matter, nitrogen, and phosphorus;

the pH is 5·9. The annual rainfall during the three seasons of the experiment was 1937–8, 26·1 in.; 1938–9, 28·8 in.; and 1939–40, 32·3 in.

The predominant grass in the area is *Trachypogon plumosus*, followed in approximate order of abundance and frequency by *Tristachya hispida*, *Elyonurus argenteus*, various species of *Eragrostis* (particularly *E. chalcantha* and *gummiflua*), *Heteropogon contortus*, *Digitaria tricholaenoides*, *Brachiaria serrata*, *Harpechloa falx*, and some less important grasses. There are various sedges and also several other monocotyledons and dicotyledons, but there are relatively few of these plants.

In spring 1937 an experiment was laid out on a piece of undisturbed original veld in this area, consisting of 16 plots each of 100 sq. yds., representing 4 different fertilizer treatments in 4 replications, arranged in the form of a Latin square:

(1) O: unfertilized;
(2) PK: receiving 400 lb. of a mixture of super- and rock-phosphate per morgen[1] and 80 lb. of muriate of potash per morgen, distributed at the beginning of the season;
(3) PK and ammonium sulphate: PK as in (2), and in addition 600 lb. of sulphate of ammonia per morgen, distributed in 3 equal quantities at suitable intervals during the growing-period;
(4) PK and sodium nitrate: PK as in (2), and in addition 790 lb. of nitrate of soda per morgen, applied in the same way as the ammonium sulphate of (3).

The total amounts of nitrogen applied were the same in treatments (3) and (4), namely 126·5 lb. per morgen.

In order to remove old growth the herbage was burnt in the winter of 1937 (before the experiment was established); at the beginning of May 1938 all herbage in the plots was cut and harvested.

In November 1938, 4 quadrats of 2 sq. metres were pegged out on each of the 16 plots, which were to receive the following clipping treatments:

(1) cut once a year (at the beginning of April);
(2) cut twice a year (in the middle of December and March);
(3) cut four times a year (in November, January, March, and May);
(4) cut at monthly intervals. Seven clippings only were possible in this treatment during 1938–9 (Nov.–May), but 9 clippings were achieved in 1939–40 (Sept.–May).

These clipping treatments were applied for two seasons (1938–9 and 1939–40), whilst the fertilizer treatments were continued in the same way as in 1937–8. Clipping was done with sickles and scissors, completely removing all herbage. The cut herbage was collected and dried at 60–70° C. Those dried-herbage samples collected over the whole season from the same quadrat were combined and weighed, and subsequently the herbage from all 4 quadrats receiving the same fertilizer-clipping treatment was mixed, ground, and stored in air-tight bottles for chemical analysis.

In August 1940 all 64 quadrats were dug up to a depth of 6 in., and the roots in this volume of soil were, as far as possible, collected. The root-material was air-dried, shoots and most of the adhering soil were removed, and the root-sample of each quadrat was weighed separately.

[1] 1 morgen = 2·12 acres.

The root-material from the 4 quadrats receiving the same fertilizer-clipping treatment was then thoroughly mixed for chemical analysis.

Nitrogen, phosphorus, and potassium were estimated in both shoots and roots. Nitrogen was determined by the Kjeldahl method modified to include nitrates. The method of determining total phosphorus has been described elsewhere [5]. Potassium was estimated by the micro-method of Brown, Robinson, and Browning [6]. The roots were also analysed for the more important groups of carbohydrates. The method of extraction and hydrolysis of sugars was essentially the same as that previously used by the writer [7]. The reducing power of the sugar and all other carbohydrate extracts was estimated by the Bertrand-Munson-Walker method [8]. Starch (including dextrin) and water-soluble polysaccharides were determined on the sugar-free residue using saliva-digestion and subsequent acid hydrolysis [8]. In the determination of acid-hydrolysable polysaccharides small samples from which the sugars had been removed were hydrolysed with 1·1 per cent. HCl for 4¼ hrs. on the boiling-water bath. The reducing power of the neutralized extract was determined and the values of starch-dextrin and water-soluble polysaccharides subtracted. Separate experiments showed that hydrolysis under the conditions described resulted in the breakdown of only negligible amounts of true cellulose. Reducing and non-reducing sugars were calculated as glucose, the other carbohydrates as glucose anhydride. The percentages of genuine plant-ash and adhering sand (silica) in the root-samples were found by treating the ash with hydrochloric acid and subsequently with a 5 per cent. Na_2CO_3 solution. All weights and constituents of roots were expressed on the sand-free dry basis.

Discussion of Results

Herbage yields.—The average herbage yields with their standard errors are given in Table 2. As early as the first season the two NPK treatments produced significant yield increases, but the PK treatment had no effect

TABLE 2. *Herbage Yields*

Grams of dry matter per two-square-metre quadrat

Number of clippings per year	O	PK	PK $+(NH_4)_2SO_4$	PK $+NaNO_3$	*Standard error*
		Season 1937–8			
1	368	333	582	590	35
		Season 1938–9			
1	474	466	905	919	36
2	543	448	856	1047	51
4	504	514	942	933	71
7	472	499	674	720	41
		Season 1939–40			
1	456	423	900	929	36
2	461	377	804	933	53
4	331	347	737	653	66
9	216	193	297	331	41

on growth. Nor did fertilizing with PK alone produce any yield increases under any of the conditions of defoliation intensity in the following two years—clearly indicating that phosphorus and potassium were limited in their effects by the deficiency of nitrogen in the soil. During 1938–9 the two NPK treatments resulted in significant yield increases under all conditions of clipping; in 1939–40 significant increases over the control and the PK treatment were obtained by the two NPK treatments only with 1, 2, and 4 clippings per year, not with 9 clippings. Thus, excessive defoliation reduced the beneficial effect of fertilizer on growth. This might be expected, since growth is a time-function. A certain length of time is required by the plants to utilize nutrients for increased growth; with frequent clippings the growth-period is much reduced. Nitrate of soda had in all cases more or less the same effect as ammonium sulphate, the differences between these two treatments being in no case significant.

During the first season in which the clipping treatments were applied increased frequency of clipping did not alter the total herbage yield in the O and PK series, but in the two NPK series 7 cuts per year significantly reduced the total herbage yield as compared with one clipping. In the following season, however, the harmful effects of frequent defoliation became more serious: 9 clippings in 1939–40 caused highly significant reductions of the herbage yield in all 4 series, whilst 4 clippings reduced the yield significantly in 3 series. It will be noted that the harmful effect of excessive defoliation was relatively more pronounced on the well-fertilized (NPK) plots than on the control or PK plots. Taking the average of all 4 fertilizer treatments the following figures give the percentage reduction caused by the various cutting treatments (as compared with 1 cut per year) in 1939–40:

Number of cuts	2	4	9
Reduction of yield, per cent.	4·4	23·3	59·6

To find an expression for the cumulative effect of the clipping treatments (as from the first season of clipping treatment to the second year) the herbage yields of the year 1939–40 were calculated as percentages of the herbage yields of 1938–9. This calculation was carried out for every single quadrat. The average figures for each fertilizer-clipping treatment are given in Table 3. Whilst with 1 cut per season the yields were

TABLE 3. *Relative Herbage Yields for 1939–40*

Yields for 1939–40 expressed as percentages of yields for 1938–9

Number of clippings per year	O	PK	PK $+(NH_4)_2SO_4$	PK $+NaNO_3$	*S.E.*
1	97·1	91·8	99·1	102·5	5·0
2	83·4	83·9	92·8	89·5	4·5
4	65·4	67·4	77·2	69·6	5·3
8*†	55·8	48·3	59·4	61·7	4·7
8*‡	46·1	38·4	43·5	44·9	5·0

* i.e. 7 clippings in 1938–9, and 9 clippings in 1939–40.
† Based on combined yields in March, April, and May.
‡ Based on yields of whole season.

substantially the same in both seasons, the yields of the other clipping treatments decreased progressively with the frequency of defoliation. The depressions in the two NPK treatments were in all cases slightly less than in the control and in the PK series, but these differences were small and mostly insignificant. The average depressions for the whole experiment were:

Number of cuts per season	1	2	4	8
Depression, per cent.	2·4	12·6	30·1	43·7

Reductions in the herbage yield due to excessive defoliation have been reported by many workers in various countries. The decreases in yield brought about by increased frequency of clipping during one and the same year may be due merely to the reduction of the growth-period, which thus does not allow for the normal accumulation of photosynthetic products. It is evident, however, that the cumulative effects of frequent clipping indicated by the falling-off in the yields from the first year of defoliation to the second season must be due to some permanent injury to the plants the nature of which will be discussed below.

Chemical composition and nutrient-uptake of the herbage.—Fertilizer as well as clipping treatments caused pronounced changes in the chemical composition of the herbage, similar to those reported by other workers [3, 9, 10, 11]. Whilst the PK treatment increased the phosphorus-content of the herbage in all cases and the potassium-content slightly in a few, the two NPK treatments significantly increased the contents of nitrogen, phosphorus, and potash under practically all conditions of defoliation (Table 4). The effects of frequent cutting were still more

TABLE 4. *Chemical Composition of Herbage*

Expressed as percentage of dry matter

Fertilizer treatment	*Number of clippings per year*	*Season 1938–9*			*Season 1939–40*		
		N	P_2O_5	K_2O	N	P_2O_5	K_2O
O	1	0·61	0·13	0·51	0·68	0·13	0·90
	2	0·91	0·21	0·89	0·83	0·16	1·50
	4	0·94	0·24	1·22	1·08	0·21	1·45
	7/9*	1·30	0·30	1·33	1·61	0·30	1·79
PK	1	0·57	0·27	0·79	0·63	0·31	0·84
	2	0·86	0·33	0·99	0·85	0·36	1·57
	4	1·06	0·40	1·03	1·10	0·37	1·54
	7/9*	1·33	0·45	1·59	1·52	0·43	1·95
PK $+(NH_4)_2SO_4$	1	1·05	0·23	0·90	0·79	0·23	1·08
	2	1·10	0·28	1·26	1·06	0·37	2·11
	4	1·36	0·36	1·44	1·36	0·34	2·04
	7/9*	1·66	0·41	2·01	1·77	0·39	2·34
PK $+NaNO_3$	1	0·87	0·22	0·94	0·90	0·23	1·11
	2	1·20	0·33	1·24	1·05	0·30	1·41
	4	1·35	0·36	1·51	1·42	0·36	1·92
	7/9*	1·49	0·37	1·59	1·82	0·41	2·29

* 7 clippings in 1938–9 and 9 clippings in 1939–40.

pronounced; the percentages of N, P, and K all increased distinctly with the increased number of clippings per season; younger herbage is always richer in nitrogen and mineral elements, whilst ageing is associated with the accumulation of carbohydrates, particularly of cellulose.

It may be concluded that fertilizer treatment and frequent clipping both resulted in considerable improvements in the quality of the herbage. Economically, however, the amounts of nutrients yielded per unit area are the more important. These yields are given in Table 5. Within limits

TABLE 5. *Nutrient Uptake of Herbage*

Grams per two-square-metre quadrat

Fertilizer treatment	*Number of clippings per year*	*Season 1938–9*			*Season 1939–40*			*Total*		
		N	P_2O_5	K_2O	N	P_2O_5	K_2O	N	P_2O_5	K_2O
O	1	2·89	0·62	2·42	3·10	0·59	4·11	5·99	1·21	6·53
	2	4·94	1·14	4·83	3·83	0·74	6·92	8·77	1·88	11·75
	4	4·73	1·21	6·14	3·58	0·69	4·79	8·31	1·90	10·93
	7/9*	6·13	1·42	6·27	3·47	0·65	3·86	9·60	2·07	10·13
PK	1	2·66	1·26	3·68	2·67	1·31	3·56	5·33	2·57	7·24
	2	3·86	1·48	4·44	3·21	1·36	5·92	7·07	2·84	10·36
	4	5·44	2·06	5·29	3·82	1·28	5·33	9·26	3·34	10·62
	7/9*	6·63	2·25	7·93	2·93	0·83	3·76	9·56	3·08	11·69
PK $+(NH_4)_2SO_4$	1	9·50	2·08	8·15	7·12	2·07	9·72	16·62	4·15	17·87
	2	9·41	2·40	10·78	8·52	2·98	16·98	17·93	5·38	27·76
	4	12·81	3·39	13·56	10·00	2·51	15·04	22·81	5·90	28·60
	7/9*	11·19	2·76	13·55	5·25	1·16	6·94	16·44	3·92	20·49
PK $+NaNO_3$	1	7·99	2·02	8·64	8·37	2·14	10·30	16·36	4·16	18·94
	2	12·55	3·47	12·97	9·80	2·80	13·17	22·35	6·27	26·14
	4	12·60	3·36	14·09	9·27	2·35	12·56	21·87	5·71	26·65
	7/9*	10·74	2·67	11·44	6·02	1·36	7·57	16·76	4·03	19·01

* 7 clippings in 1938–9 and 9 clippings in 1939–40.

increased frequency of clipping raised the total yields of nitrogen, phosphorus, and potassium. In the first season maximum recovery of these elements was reached in the O and PK series with monthly defoliation, whereas in the two NPK series the highest yields of nutrients were obtained in nearly every case with 2 and 4 clippings per year, monthly cutting resulting in a reduction of the total recovery of nitrogen, phosphorus, and potassium. In 1939–40 the harmful effects of excessive clipping became much more pronounced—monthly clipping resulting in very distinct reductions of the total nutrient yields in all series. The total yields of nutrients were always appreciably higher on the NPK plots than on the O and PK plots, maximal amounts being recovered on the well fertilized and moderately clipped quadrats. A noteworthy feature is that the mere addition of nitrogenous fertilizers to phosphates and potash salts resulted in an increased utilization of phosphorus and potassium, as indicated by their total uptake.

Root-weights.—Table 6 shows the root-weights in grams of sand-free dry matter per 2-square-metre quadrat. In all four fertilizer treatments these distinctly decreased with the frequency of clipping. Though most of the intermediate differences are statistically insignificant, cutting at monthly intervals in all cases brought about significant reductions in

the root-weights if compared with those obtained with one harvest per season. None of the fertilizer treatments had any pronounced effect on root-development, which was rather unexpected, since increased nutrient

TABLE 6. *Weight of Roots*

Grams of sand-free dry matter per two-square-metre quadrat

Number of clippings per year	O	PK	PK $+(NH_4)_2SO_4$	PK $+NaNO_3$	*Average*	*S.E.*
1	583	418	556	592	545	±47
2	483	385	433	567	468	±38
4	286	256	448	366	340	±36
8	204	217	177	204	197	±23

supply when beneficial to top growth has usually been found to promote root-growth also, though to a less extent. On the other hand various workers have demonstrated that nitrogen supply, whilst fostering top growth, may aggravate the harmful effects of intensive defoliation on root-development.

As many grasses send some of their roots down to a considerable depth, the reported weights of the roots recovered from the upper 6 in. may not be representative. Additional experiments made by the writer have shown, however, that the bulk of the roots rapidly decreases in lower soil layers. Thus, in one case, when a quadrat was dug out to a depth of 12 in., the layer from 6 to 12 in. was found to contain only one-tenth of the root-bulk contained in the upper 6 in. Hence the reported values of root-weights may be regarded as reliable and representative. Owing to the relatively large variations of the root-weights within one and the same series, however, smaller differences, such as those due to fertilizer treatment, may not have become detectable. The fact that in this experiment fertilizers had no apparent effect on the root-weights may, thus, be due to inaccuracy or to the particular conditions of this experiment. It may, however, certainly be concluded that measurable effects of fertilizers on root-development should not necessarily be expected in every case where the same treatments significantly influence the herbage yield.

The average figures and corresponding standard errors are given in Table 6. The root-weights showed marked and significant reductions by increased clippings. Reduction of the root-system as a consequence of excessive defoliation has been reported by many workers in various countries, and some authors have shown that similar effects are produced by heavy or excessive grazing.

Chemical composition of the roots.—From Table 7 it may be seen that the percentages of reducing sugars, non-reducing sugars, and starch in the roots decreased with the intensity of defoliation. The percentages of reducing sugars were rather low. Non-reducing sugars were generally found in amounts 4 to 5 times as high. The percentages of starch were in all cases intermediate. The two NPK treatments appear to have increased the sugar-content in most cases, whereas the starch-content was reduced by all three fertilizer treatments.

TABLE 7. *Chemical Composition of Roots*

Expressed as percentage of sand-free dry matter

Fertilizer treatment	*Number of clippings per year*	*Reducing sugars*	*Non-reducing sugars*	*Starch*	*Sugars and starch*	*Water-soluble polysaccharides*	*Acid-hydrolysable polysaccharides*	N	P_2O_5	K_2O	*Ash*
O	1	0·49	2·73	1·86	5·08	0·28	16·7	0·52	0·10	0·47	3·52
	2	0·42	2·38	1·77	4·57	0·37	16·1	0·56	0·12	0·50	3·62
	4	0·43	2·25	1·73	4·41	0·09	14·1	0·55	0·12	0·51	3·81
	8	0·36	1·50	1·13	2·99	0·06	16·3	0·58	0·12	0·39	3·11
PK	1	0·52	2·78	1·50	4·80	0·00	15·9	0·49	0·16	0·43	3·97
	2	0·43	2·55	1·41	4·39	0·13	14·0	0·52	0·19	0·47	3·75
	4	0·41	2·12	0·78	3·31	0·10	17·8	0·55	0·19	0·48	3·55
	8	0·30	1·48	0·82	2·60	0·31	14·5	0·55	0·13	0·36	3·37
PK $+(NH_4)_2SO_4$	1	0·60	3·16	1·65	5·41	0·39	16·2	0·81	0·20	0·52	3·32
	2	0·69	3·25	1·24	5·18	0·34	15·7	0·71	0·18	0·48	3·31
	4	0·64	2·39	1·21	4·24	0·12	15·9	0·77	0·19	0·43	4·46
	8	0·56	2·08	0·85	3·49	0·29	16·0	0·77	0·14	0·38	3·21
PK $+NaNO_3$	1	0·46	2·79	1·44	4·69	0·27	15·5	0·79	0·21	0·43	3·59
	2	0·45	3·13	1·59	5·17	0·10	16·7	0·73	0·20	0·54	3·47
	4	0·61	2·62	1·38	4·61	0·37	16·1	0·75	0·17	0·36	3·15
	8	0·44	1·86	1·22	3·52	0·36	15·6	0·76	0·16	0·37	2·83

Water-soluble polysaccharides occurred only in very small amounts showing no direct relation to any of the treatments. Acid-hydrolysable polysaccharides were found to form a rather large proportion of the root-tissue (14–18 per cent.), but remained more or less constant under all conditions of clipping, apart from certain irregular fluctuations which must be considered to be due to certain errors inherent in the method of determining these substances.

Whereas the nitrogen-content of the roots was not appreciably affected by different frequencies of cutting, monthly defoliation reduced the percentages of potash, phosphorus, and to a less extent the total ash-content; in the O series, however, the low percentage of phosphoric oxide remained at a more or less constant level. The nitrogen-content of the roots was raised by the two PNK treatments and the percentage of phosphorus by all three fertilizer treatments.

Storage and exhaustion of root-reserves.—Various workers [7] have shown that in many herbaceous plants, including grasses, carbohydrates as well as nitrogen and mineral elements are, towards maturation, translocated from the aerial parts to the roots or other underground systems. There they are stored over winter to be drawn upon for the production of new shoots in the following growing-period. Corresponding seasonal chemical changes in the roots of some of the most important South African Highveld grasses, i.e. an increase in these substances in the roots in autumn and winter and their decrease in spring and summer, have been demonstrated by the writer and other workers [5, 14]. Since translocation from shoots to roots takes place mainly after flowering and during maturation, such storage is naturally prevented with clipping at frequent and short intervals. On the contrary, excessive clipping will, by its frequent repetition of the shooting process, cause an increased utilization and upward translocation of organic root-reserves. Hence excessive defoliation will ultimately result in a depletion of these organic reserves in the roots. This not only explains the decline in vigour with frequent clipping as indicated by the progressive reduction of herbage yields, but also the reduction in root-weights and the decreases in the percentages of sugars and starch in the roots.

With increased defoliation intensity these substances decreased in the roots not only in percentage but even more in actual amount (Table 8).

TABLE 8. *Combined Amounts of Sugars and Starch in Roots*

Grams per two-square-metre quadrat

Number of clippings per year	O	PK	PK $+(NH_4)_2SO_4$	PK $+NaNO_3$	Average
1	29·6	20·1	30·1	27·8	26·9
2	22·1	16·9	22·4	29·3	22·4
4	12·6	8·5	19·0	16·9	14·3
8	6·1	5·6	6·2	7·2	6·3

Clipping at monthly intervals reduced the total dry matter in the roots on an average by 63·8 per cent. as compared with one clipping per year.

The combined amounts of sugars and starch were reduced by 76·6 per cent. For this reason sugars and starch must be regarded as important storage materials. The acid-hydrolysable polysaccharides, which represent a rather heterogeneous group of carbohydrates (often referred to as 'hemicelluloses'), appear to be largely structural materials. As such they cannot be utilized by the plants as food reserves, and hence remain more or less unaffected in percentage by frequent clipping.

During the two years in which the clipping treatments were applied actual growth of the root-systems may have taken place in the more protected plants. The total reduction of dry matter and constituents of roots in the more frequently clipped plants is most probably due not only to the prevention of the normal process of storage, and to excessive utilization of available root-reserves, but also to the dying-off and subsequent decomposition of weakened and starved root-tissues.

The decrease in phosphorus and potassium in the roots of the more frequently clipped plants cannot be due to a depletion as in the case of sugars and starch, since the figures for total nutrient uptake of the herbage (Table 5) indicate that the highest amounts of phosphorus and potassium were removed in the herbage not with monthly defoliation but with 2 or 4 clippings per year. This was more particularly so in the two NPK series, whilst in the PK series the total uptake of phosphorus and potash by the herbage remained far below that in the two NPK series, even though the same amounts of phosphorus and potassium were available. The observed reduction in the percentages of phosphoric oxide, potash and total ash under conditions of excessive defoliation must thus have other reasons, such as a decreased rate of absorption or actual losses from weakened or dead roots.

Summary and Conclusions

Summing up the results of this investigation it may be said that the quality of the herbage was improved by fertilizer treatment as well as by shortness of intervals between successive harvests. But these desirable effects of frequent defoliation were largely offset by the simultaneous decline of the herbage yields with more frequent clipping, and the consequent reduction in the total yields of nutrients in the herbage per unit area. Moreover, the beneficial effect of fertilizers on growth was largely reduced under conditions of excessive defoliation. Maximal amounts of nutrients per unit area were recovered from well fertilized and moderately clipped veld. Frequent defoliation resulted in a permanent injury to the vigour and power of regeneration of the plants, which was not checked by fertilizer treatment. Lastly, it was shown that the damage done to the plants by frequent defoliation was associated with corresponding reductions in the root-weights and depletion of root-reserves. Here again, fertilizer treatment was not able to counteract the damage to root-development and the exhaustion of root-reserves.

It was indicated in the beginning that the effects of clipping differ in various ways from those of grazing. Thus, whilst in the experiments reported here the herbage was completely removed with each cut, the

grazing animal does not usually completely defoliate the plants, though occasionally whole plants are pulled out and uprooted. Defoliation by the grazing animal is largely selective, so that more desirable species of grasses are affected to a higher degree than less palatable ones; and in addition the results of trampling and manuring must be considered. It is to these effects of the grazing animal that changes in the botanical composition of the veld are largely due. Such effects are clearly not included in clipping experiments, so that clipping should certainly not be regarded as a true imitation of grazing.

On the other hand a high degree of grazing intensity is always associated with and practically tantamount to a high degree of defoliation, so that the effects of clipping must be at least similar to those of grazing. In fact, recent grazing experiments, carried out in the same area, have given results (to be published later) very similar to those reported above, confirming many of the conclusions drawn from this and other clipping experiments.

Whilst no concrete detailed proposals as regards actual grazing management can be made based on the results of such clipping experiments alone, it is hoped that the present contribution may help to elucidate some of the fundamental principles the understanding of which is essential for any sound pasture management in the future.

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RECENT RESEARCH IN POTATO BREEDING

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A NEW era in potato breeding may be said to date from the recognition of the existence of Wart Disease in scattered localities throughout England, and the discovery of immune varieties in 1908 by G. C. Gough [1]. Little progress to combat the new danger was made until, under the pressure of war in 1915, the importance of the potato as a foodstuff was vividly brought home to a public hitherto accustomed to regard the entire world as its larder.

The Influence of Wart Disease on Potato Breeding

The best of the varieties of the day had proved to be susceptible to the new disease. Amongst them, the first earlies, Epicure, Sharpe's Express, May Queen, Ninetyfold, Early Rose, and Duke of York; the second early, British Queen; the main crops, Up-to-date and King Edward; and the late, Magnum Bonum.

One of the first and most essential measures necessary for dealing with the new and serious situation was to determine how many of the named potatoes in cultivation were in reality distinct, and how many were mere fanciful synonyms of old and established varieties. Unless that was ascertained, no advice to growers as to what was to be grown and what avoided could be given. A committee set up originally by the Royal Horticultural Society in 1915 under John Snell, and since 1920 carried on by the National Institute of Agricultural Botany under the chairmanship of the writer, showed that the greater proportion were in fact, synonyms, the variety Up-to-date, for example, being known and grown under close on 200 different aliases [2].

The whole potato industry was obviously threatened should the disease spread before adequate quantities of suitable immune varieties were to hand. The occasion called for raisers possessed of the flair of the past masters, coupled with a knowledge and appreciation of the important lessons which scientific horticulture, and in particular the new Mendelian doctrine, could impart. The right men were not wanting, foremost amongst whom is Donald McKelvie, of Lamlash, Isle of Arran, Scotland, a man of outstanding ability and knowledge, with a genius for 'spotting a winner', to which his modesty, patience, and generosity form a worthy setting. Another breeder of outstanding ability is Mr. John Watson, a partner of Messrs. McGill & Smith, Ayr, whose Doon Early (1934), Gladstone (1934), and Doon Eire (1940) give promise of enduring merit.

In Mr. John Clarke of Broughgammon we have a raiser who combines in an exceptional degree a wide scientific knowledge of all that concerns the potato, both domestic and wild, with a remarkable genius for hybridization and plant-raising. His Ulster Chieftain promises to be a valuable addition to the all too few wart-immune earlies at our disposal.

Potato breeding from now on was directed towards combining im-

munity to wart disease with tolerance or resistance to virus disease, and the superimposing of both on such recognized desirable qualities as smooth, oval-to-kidney shape, shallow-eyed tubers, possessed of a white flesh and a floury texture.

The life-history of the fungus causing Wart Disease (*Synchitrium endobioticum*) and the character of its attack on susceptible and immune sorts, respectively, had been vigorously pursued. The former notably by Curtis [3], and the latter by Köhler [4, 5, 6, 7].

The inheritance of the quality in the potato which determined resistance or susceptibility to the attack of wart fungus was studied by the writer and J. W. Lesley [8, 9], who showed that it was controlled by genes acting on relatively simple Mendelian principles. Breeders had also at their disposal detailed knowledge as to the genetic inheritance of such characters as tuber colour and shape, depth of eye, and maturity [10], and an ever-growing knowledge as to the immunity or otherwise to wart disease of existing varieties.

This latter work was carried out by the National Institute of Agricultural Botany, whose activities have done so much to improve the standard of potato varieties and potato growing in Great Britain. It also provided raisers with facilities for the rapid testing of first-year seedlings at Ormskirk. Thus equipped, breeders like McKelvie were able to make an immediate choice of suitable parents and at the same time eliminate susceptible offspring without loss of time. As a result, there has been introduced within a few years a large number of good wart-immune varieties which have allowed growers in the infected areas freely to carry on their industry. Notable amongst Mr. McKelvie's many productions are a first early, Arran Pilot; an early main crop, a very heavy cropper, Arran Banner; a late variety and an excellent keeper, Arran Consul. A good immune second early is to be found in Dunbar Rover, raised by T. Spence of Dunbar.

Virus Disease and the Degeneration of Potato Varieties

Plant-virus research may be said to have been initiated in Great Britain in 1920, though only a few people had by then realized the importance of the subject. It was in that year that Dr. Kenneth Smith was appointed in Manchester to investigate the subject from the entomological side, and in the following year an International Conference on the Potato was convened by the Royal Horticultural Society. Virus diseases occupied much of the time at the conference. On this occasion it was shown [11] that the cropping capacity of seedlings derived from self-pollinated plants of any given variety was controlled by genetic factors, and that, no matter how degenerated by virus infection the parent plant was, the cropping capacity of its seedlings was in no way affected; hence it was evident that the loss in crop return of the parent plant was not due to senescence, or the degeneration of the variety, but was directly due to an infection which spared the sex cells. Prof. H. M. Quanjer [12] of Wageningen, one of the pioneers in plant-virus research, showed how the various types of infection of the potato might be differentiated, and came to the same conclusion as Paul Murphy [13].

who had just commenced his research in Dublin, that the virus diseases were induced by parasitic ultra-microscopic living organisms.

In the next few years the Ministry of Agriculture became increasingly concerned with the degeneration of potato varieties and the necessity for research. The larger producers were worried about the unsatisfactory cropping of many of their trusted varieties. Sir Daniel Hall [14], at that time the Scientific Adviser to the Ministry, feeling that the time was ripe for a direct attack on the subject, in 1926 advised the Ministry to establish a research station under the directorship of the writer, to be devoted to the study of virus diseases of the potato. From then onwards the problem of virus infection in the potato and other plants of economic interest has been undertaken in most of our leading horticultural stations. Great progress has been made both in our knowledge and practice, both here and abroad.

The immediate reaction of the new interest in virus diseases was to direct the attention of potato-variety raisers to the problems of creating varieties, which might possess some innate constitutional mechanism that would protect them against attack. That the effect was worth while can be seen by the general upward trend of the returns of the tonnage per acre of the nation's potato crops. It is made still more evident when it is remembered that the crops of potatoes from a healthy vigorous stock of, say, Majestic, may easily reach 14 tons per acre; whilst one from a stock of the same variety badly infected with Leaf Roll may not reach 4 tons per acre.

Before 1920 it would be safe to hazard the statement that in Great Britain the annual loss of potential crop due to virus infection was at least 25 per cent. of that actually harvested, a loss in money value of many millions of pounds each year. During the last 10 years that loss has been very considerably reduced—notably by the use of healthier seed and better varieties.

Research, especially that initiated in the Potato Virus Research Station at Cambridge in 1926, had shown that certain varieties of potatoes which may have every appearance of perfect health may be saturated with a virus which, if communicated to a susceptible variety, would bring about its destruction. So long as the hidden infection is not readily conveyed by contact or by insects, no harm need ensue. Notable examples are the Streak, or Virus 'B' in Up-to-date, discovered by Murphy, and 'Paracrinkle' in King Edward by Salaman and Le Pelly. When, however, the tolerant host plant carries a virus such as Leaf Roll, as the Swedish variety, Imperia, may do, or the Virus 'A', as Murphy showed Golden Wonder always does, both of which viruses are conveyed to healthy plants by aphides, then their presence in the potato field is a serious danger to other varieties growing in the neighbourhood.

The virus known as the 'X' virus, of which the less virulent forms may be carried by many of our best varieties without obvious symptoms, is easily transmitted to healthy plants by leaf-contact brought about by the action of the wind in the field. Infection by the 'X' virus in some varieties may have no ill effects; in others it may to a greater or lesser extent weaken the plants without seriously crippling them.

The growing plants often lack robustness and vigour, and yet present no recognizable symptoms of disease. This condition was studied by the writer in the growing crop, especially that of Arran Signet, in which infection with the 'X' virus is common. The degree to which the plants suffered, varied with the strain of 'X' present, from almost perfect health to varying stages of unthriftiness. It was rarely that one saw plants obviously mottled and sickly. Yet such infection, which may elude the eye, may well account for a loss of 2–4 tons per acre. This type of infection is of particular importance because it is impossible to eliminate all affected plants by roguing. For this reason even the best accredited seed may belie its certification when brought down south for growing.

Virus-Resistant Varieties

The Scottish Society for Research in Plant Breeding has put on the market a variety, Craig's Defiance, which is immune to both the viruses 'A' and 'X'. Actually, several existent varieties are equally so, to one or other, or both. The immunity is a peculiar one. It is not that the varieties are immune: on the contrary, they are so intensely susceptible that if artificially infected as young plants they die off immediately. Presumably, in the field, the reaction of the plant at the spot at which infection takes place becomes at once necrotic and shuts off the paths by which the virus might obtain access to the remainder of the plant.

In recent years plant breeders in America have succeeded in producing new varieties which may be resistant to attack by the 'X' virus, or entirely immune to its infection, as is the variety known under the number 41956. The resistant varieties have been raised from ordinary domestic stocks and they include the earlies, Earlaine, Masarba, and Warba; and the main crop varieties, Katahdin, Chippewa, and Huma. A recent introduction is Sequoia, for which is claimed resistance to *Phytophthora infestans*, as well as to the attack of leaf-hoppers and flea-beetles. Of these varieties, Katahdin has been used in the Cambridge Research Station: it is not immune to the 'X' virus, but it does exhibit some resistance to infection. In the field Katahdin does well, but it is as susceptible as most others to both Leaf Roll and the 'Y' virus.

The variety No. 41956 is exceptional: one cannot succeed in infecting it with the 'X' virus, whether by abrasion, needling, or grafting. Its origin becomes therefore a matter of profound interest. It was bred by C. F. Clarke, Horticulturist, Division of Fruit and Vegetable Crops, Bureau of Plant Industry, U.S.A. Its maternal grandparents are the variety Villareola; its paternal grandparents the domestic variety Aroostock Wonder and Flourball. Villareola is a variety of *S. tuberosum* from Chile, and presumably it is from it that No. 41956 derives its immunity.

The two most serious virus diseases of the potato in this country are Leaf Roll and that caused by the 'Y' virus which commonly produces Leaf-drop Streak. To neither of these diseases have we as yet any immune varieties. It may be mentioned that K. O. Müller of Dahlem, Germany, informed the writer in 1938 that he had raised a variety,

partly of Chiloean parentage, which was highly resistant to the 'Y' virus. A good economic variety thus endowed would be a most valuable weapon in the struggle for better crops. In the Imperia mentioned above we have a carrier of Leaf Roll; and in Edgecote Purple, an otherwise valueless variety, a carrier of the 'Y' virus. Inasmuch as these two viruses are conveyed by aphides, it is obvious that their carriers must be rigorously excluded from our potato fields.

Another avenue of approach towards the maintenance of the health of our potato stocks was opened when it was shown [15] that plants may be vaccinated with a weak and harmless variant of the 'X' virus, and thereby gain protection against the more virulent and harmful strains. This species of protection occurs in nature without the intervention of man, in several of our domestic varieties of potato, of which Up-to-date is a good example. A similar protection by vaccination was obtained with the 'Y' virus [16], but the use of such a vaccine has not passed beyond the experimental stage. It is, moreover, very doubtful whether it would be a safe or desirable method of protection for use in the field.

The Influence of Recent Russian Discoveries on Variety Production

A revolution in our ideas as to the origin and the botanic status of the potato, which, so far, has not affected the practice of its cultivation except in the Arctic Circle in the U.S.S.R., followed the classic work of the Russian savants. Three expeditions were sent to South America, Central America, and Mexico between 1926 and 1932, in the course of which a large number of hitherto unknown tuber-bearing Solanums were discovered. Some of these, which were cultivated by the natives of the high Andean plateaux and valleys, were but distantly related to our domestic potato. The most widely extended species, however, was *S. andigenum*, a highly variable species, which occurs from the Argentine to Central America. The potatoes of Chile and Chiloe the Russians claim to be true *S. tuberosum*, and the ancestral form of our European domestic potato, a view which is not accepted by the present writer. Their labours have done much to broaden our outlook on the origin of the potato and, indirectly, to increase our knowledge of its earliest cultivators. But what, perhaps, appeals most to those interested in the scientific aspects of potato cultivation, is the knowledge that potato breeding need no longer be confined to the ringing of the changes on the limited number of characters presented by the domestic varieties in cultivation. Indeed, a host of new qualities has floated into our ken. The potato has become suddenly plastic, and gives promise of being moulded to suit the most diverse requirements of industrialized man.

The Mutability of the Potato Tuber

The plasticity of the common domestic potato has been demonstrated in the most dramatic manner by T. O. Asseyeva [17, 18]. She showed that many of our varieties, more especially those with parti-coloured skins, were in reality chimeras, and that by a simple surgical manipu-

lation of the tuber buds, the potato plant could be turned literally inside out, like a glove. Some coloured tubered varieties can be converted into white-skinned ones, and vice versa. Although this phenomenon has little, if any, industrial value, its discovery has shed much light on the behaviour of many of our varieties. The sudden and not infrequent appearance of somatic mutants in the field, which may differ from the parental type only in the colour or texture of the tuber skin, or the shape of the leaflets, now finds its explanation. The case of Sefton Wonder and Great Scot, Field Marshal and Up-to-date, are examples of chimeras, in which a change from a smooth to a russeted skin has occurred, probably as the result of accidental damage to the eye of a seed tuber in the field. Colour change of a similar nature, as well as the changes in genetic constitution of the sex cells, may also be brought about; such have been studied in the variety Arran Victory [19, 20].

A further example of the plasticity of a variety is to be seen in the manner in which its maturity may be advanced. For a hundred years or more growers have been accustomed to 'sprout' their early potatoes, whilst some treat their later varieties in the same way. The exposure of the tuber to the light, in open trays, in the early days of spring, has also the advantage of maintaining them at a higher temperature than they would experience in the clamp. The effect of both these agencies is to advance the growing-period and tuber-formation of the plant within the season.

Lysenko described, under Vernalization, a method of advancing the vegetative growth of the potato, which consists in suspending tubers under strong and continuous illumination at temperatures between 15° and 20° C. The method is not suitable for large-scale work and when tried has failed to produce any notable result [21]. Whilst in principle the method is similar to the common one of sprouting, it differs fundamentally from Lysenko's vernalization of cereal seeds.

The dormancy of the potato may be broken at once in any variety, by chemical or physical means. Exposure of tubers to the vapour of ethylene chlorhydrin, or the steeping of them in sodium thiocyanate, are two of the most effective methods devised by Denny [22, 23, 24] in his valuable research on this question. Removing the skin of a tuber brings dormancy to an end, and greatly hastens the growth of the sprout. A single eye with a naked core of tuber flesh attached will develop into a plant with amazing rapidity [25].

New Sources for the Creation of Specialized Varieties

As the examination of the Russian collection proceeded, it was obvious that material was to hand by which there might be built up varieties specially designed to serve man's needs in the widest and most varied manner. Thus we might contrive one variety of potato which would withstand the cold and give us food in subarctic conditions; another which would do the same in subtropical climes. Some varieties might be built up to be particularly rich in starch, for industrial purposes; another, rich in protein, for dietetic use. Foremost in the minds of breeders in every land will be the desire to secure, at long last, varieties

resistant or immune to the chief diseases and pests which afflict them; against Blight, Wart Disease, Virus infection, and insect troubles, especially the Colorado Beetle.

Blight-resistant Varieties

The creation of resistant varieties prior to the war was proceeding in the following countries in order of priority: England, Germany, Russia, the U.S.A. A short description of the writer's efforts will give some idea of the character of the work. Similar experiences have been recorded by the German worker, K. O. Müller [26, 27, 28], who, in 1921, took over the species crosses Broili had made in 1918.

Resistance to the attacks of *Phytophthora infestans* displayed by *S. edinense* and its seedlings was shown to have a genetical basis as early as 1908 [29]. This was followed in 1914 by the discovery that a similar resistance existed in *S. demissum* [10]. From that time breeding for blight-resistance proceeded at Barley, Herts., till it was transferred to

Pedigree of a New Variety bred for Resistance to Wart Disease and Blight, and of a Good Table-quality

Generation	*Matings*	*Remarks*
I	*S. demissum* × Seedling of domestic type	A combination of Resistance to Blight and No Yield with susceptibility to Blight; very high yield, white, but indifferently shaped tubers.
II	Selfed	Selection of the most vigorous types with best yields. Crops small and tubers of poor shape and size.
III	Selfed	Continuance of selection, some better crops secured.
IV	× Domestic seedling	Strengthening of the domestic characters of haulm and tuber. Selection of most desirable types with much improved yields.
V	Selfed	Further selection on same lines, with elimination of all blight-susceptibles.
VI	Selfed	Continuance of selection and elimination of blight-susceptibles.
VII	× Sutton's Abundance	Introduction of resistance to Wart Disease and improved table-qualities. Selection for resistance to Wart and Blight.
VIII	× Katahdin	Introduction of resistance to Virus 'X' infection, and continued selection.
IX		Several seedlings combining blight-resistance, wart-resistance, and possibly resistance to Virus 'X', with good economic qualities.

Cambridge in 1926, when the writer was assisted in the work by Miss C. O'Connor. A typical pedigree of one of the many lines raised is given above (p. 131). From it will be seen how resistance to wart disease and good table-quality were introduced by the use of the variety Abundance, and how Katahdin was brought in to the pedigree in order to give some resistance against Virus 'X'. The domestic seedlings employed were selected because they were exceptionally heavy yielders and had, in the course of another research, been shown to transmit this quality to their offspring. Throughout, a rigorous selection was exercised, in favour of seedlings with good yield, well-shaped, fleet-eyed, white- or faintly coloured-skinned tubers, and against those with long and abundant stolons, numerous but small tubers, and ill-furnished, stiff, and non-covering haulms.

The first cross could only be made if *S. demissum* was used as the female parent, and the F1 generation, apart from its resistance to Blight, gave no promise of any economic value, but by selfing and back-crossing, useful seedlings were obtained in later generations.

The resistance offered by these seedlings was for several years complete both in haulm and tuber, but in 1932 there were signs that the stocks were no longer completely immune: by 1936 they succumbed to blight, but nearly 6 weeks later than had the main crops King Edward and Majestic. It was evident that we were dealing with a new biotype of the fungus; this was subsequently isolated in pure culture. It was now necessary to find a fresh potato source which was immune to the new type of blight. By testing the various wild and other forms at the Station Miss O'Connor succeeded in finding a non-domestic potato which, wrongly named Aya Papa, was undoubtedly a derivative of a *S. demissum* hybrid stock. This stock proved to be completely resistant to both the common and the new biotype of the fungus. From it a new series of crosses with suitable domestic parents, as well as the previous resistant seedlings, was made, forms resistant to both the common and the new strain of the fungus selected, and further back-crosses made. In order to test the susceptibility of large numbers of seedlings to the two strains, special methods were developed by the writer, Mr. L. Selmes, head-attendant, and Dr. M. L. R. Petterson of the Station, which enabled positive results to be obtained within 5 days. The results are promising, but it is realized that in England, unless the new resistant variety is as good in every respect as the best of our current varieties, it will not be accepted by the farming community because of its resistance to blight, at least under existing conditions.

Past Experience and Future Promise

It would be a mistake to think that the use of wild species for hybridization with the domestic potato is something new. Klotsch [30] in 1850 hybridized the common potato with the pollen of *S. demissum*, then known as *S. utile*, and studied the F1 generation with much care, noting its extreme lateness and its freedom from blight. Blanchard [30] produced one seedling by fertilizing *S. ohrondii* with the pollen of the domestic potato, but that came to nothing. Arthur Sutton set out to

breed a disease-resistant variety and crossed *S. maglia* with pollen of the common potato; he obtained two seedlings, both highly susceptible to blight, a fact which to-day gives rise to no surprise, seeing that *S. maglia* is itself intensely susceptible. The Rev. Aikman Paton [31], early in this century, crossed domestic varieties with some half-dozen wild species, and raised a few seedlings of the first generation but made no further use of them.

Dr. J. Wilson, of St. Andrews University, in the early years of this century, made many attempts to employ wild species in his breeding, in order to obtain resistance to blight, but he had no success because he had not access to suitable wild types. As has been mentioned earlier, successful crosses between domestic types and *S. edinense* and *S. utile* were made by the writer.

The Russian work, however, has an importance of its own because of the generous scale on which it was conceived, and the painstaking manner in which it was carried out. The taxonomic and genetical studies of the material have already yielded results which bid fair to give these expeditions a unique position in the history of man's exploitation of nature.

Whilst Russian workers are justifiably proud of the discovery of so much new material, there has been a tendency to entertain false hopes of immediate and important economic results, forgetting how long and difficult is the road, which separates, rather than links, the potential gifts of nature with the finished economic product society demands. In no case is this truism more clearly exemplified than in that of the potato. Recently, criticism and disappointment have been expressed in Russia itself at the meagre economic results which have so far accrued, and workers are warned that more important results are to be expected from the cultural methods inspired by Lyssenko than by the pursuit of perfection along the tortuous and rocky by-ways of genetic research [32].

Notwithstanding, it would seem more probable that progress in the breeding of new potato varieties will be made by the geneticist, analysing, and subsequently recombining, the new qualities he has culled from a number of wild species and varieties, even if his most difficult task is the elimination of the undesirable characters which have crept in with the new blood. This is not to say that the selectionist, with that flair, akin to genius, for choosing the most promising from a host of competitors, will not still have much to say in the final choice. It is he who will decide which plant exhibits that combination of desirable qualities which best serves a particular set of economic requirements. Potato breeding promises to be the most exciting pursuit open to the horticulturist.

We may now proceed to enumerate some of the demands which are being made to-day on the potato breeders, and the sources in which he may expect to find the essential qualities he is seeking, qualities which, by skilful breeding, he may hope to transfer to the domestic potato. In the main, the demands fall into two classes: the one which seeks for physiological conditions on the part of the plant, to enable it to prosper under special climatic and soil conditions, and the other which seeks to endow the plant with such qualities as will protect it against insect pests and fungoid and other diseases.

In the following paragraphs an attempt is made to set out the characters which are desired in one column, and the sources which have been found by researchers to be endowed with one or more of the characters in question in another. Such sources, more often than not, occur in wild species but distantly related to the domestic potato, and these frequently possess many objectionable features which the breeder may find difficult to eliminate from his hybrid cultures. This, however, need not dismay him. If it is possible to eliminate such qualities as almost complete absence of crop, extreme length and number of stolons, purple skin, and irregularly shaped minute tubers, from crosses with *S. demissum*, and yet retain the essential quality, resistance to the attacks of *Phytophthora infestans*, which *S. demissum* bestows, it should not be impossible to do the same with such other wild types as are the possessors of equally desirable characters.

To meet Physiological Requirements

Characters required	*Source*
Tropical and sub-tropical climes:	
(*a*) Short-day habit for tropics	*S. andigenum* (2*n* = 48[1]) and most of its varieties
(*b*) Resistance to drought	*S. Antipoviczii* (2*n* = 48) *S. ajuscoense* (2*n* = 48) *S. medians* (2*n* = 36) Bukasov in 1934 [33] stated that *S. Vavilovii*, which grows on the rainless Peruvian coast, was highly drought-resistant; later he found that it had no such resistance.
(*c*) Prolonged dormancy of tuber sprout	*S. Vavilovii* (2*n* = 24) *S. commersonii* (2*n* = 36)
Arctic latitudes:	
(*a*) Long-day habit	Most European domestic varieties. Some varieties of *S. andigenum* in long-day and cool conditions yield well.
(*b*) Early maturity	Numerous European varieties [34] *S. Rybinii* (2*n* = 24)
(*c*) Short dormancy	*S. Rybinii* *S. Kesselbrenneri* (2*n* = 24) [34]

Long-day environment, which militates against tuber-formation in many wild species, is counteracted to the advantage of tuber-formation, by low temperatures, and dry conditions of growth.

Cool climate, Night Frosts, Mountain Heights:	
Frost resistance	*S. acaule* (2*n* = 48) [34, 35] (will withstand −8° C. without damage) *S. curtilobum* (2*n* = 60) [34] (said to give very promising results in domestic crosses) *S. Millanii* (2*n* = 36) [34] *S. Juzepczukii* (2*n* = 36) [34] *S. ajanhuiri* (2*n* = 24) [34] For methods of testing see Stelzner [36].
Early maturity	The best European early varieties *S. Rybinii*
Early and rapid growth of tuber and short growing-period	*S. boyacense* (2*n* = 24) *S. Kesselbrenneri*

[1] The formula 2*n* = 48, &c., refers to the somatic complement of chromosomes.

Characters required	*Source*
Late maturity:	
(*a*) Late development of tubers	A few European varieties such as Arran Consul and Dunbar Standard
(*b*) Timely development of tubers with long continued growth	Most of the late European varieties
(*c*) Late development of tubers follows the attempt to grow short-day varieties, such as most of the Andigenums, in a long-day environment.	
Late planting, following on a winter catch-crop	
Rapid and good growth under short-day conditions, prolonged dormancy, and resistance to *Phytophthora infestans*	Variety BRA 5/31 of K. O. Müller [38]
Humid atmosphere, Boggy lands:	
Tolerance of excessive moisture and heat	*S. phureja* ($2n = 24$) *S. goniocalyx* ($2n = 24$) *S. commersonii* ($2n = 36$)
Such lands are, in general, unsuitable for high-yielding varieties.	
Two crops per annum:	
Quick growth Early maturity	*S. Rybinii*
Short dormancy	*S. phureja*
High starch-content	*S. phureja*
Generally correlated with a low protein-content	*S. andigenum* back-crossed by *S. Rybinii* has given a high percentage of starch. *S. andigenum* × European varieties generally give low values but some *S. andigenums*, e.g. Herrera, are said to have given hybrid seedlings with 26 per cent. starch [39]. In general, crosses with *S. andigenum* varieties are not rich in starch and may be very low. Better results with *S. andigenum* varieties *Cuzcoense*, *sihuanum*, *tolucanum*, *caiceda*, and *hederiforme* [37] are recorded. *S. semidemissum* and *S. demissum* hybrids with *S. tuberosum*, and their back-crosses may develop very high starch-values [39].
High protein-content	*S. demissum* ($2n = 76$) [39] *S. phureja* *S. semidemissum* ($2n = 60$) [40]
High dry-matter content	Varieties Donwe Jan, Lützow, Glückauf, and Mathis, used as parents with wild varieties give values up to 30 per cent. [39]
Low dry-matter content	Centifolia and Katahdin used as parents with wild varieties give low values [39].
Vitamin-C content	All domestic varieties. Centifolia said to contain 9 mg. per gm. Epicure and Great Scot 6 mg. per gm., respectively *S. Antipoviczii* ($2n = 48$), var. *gandarae* form *densipilosum* ($2n = 48$) is said to be exceptionally rich [41]. Values up to 50 mg. per gm. have been found in some Andigenum varieties [72].

Characters required	*Source*
Darkening of uncooked potato: For the preparation of dried potatoes	Frühgold darkens least, Parnassia darkens most [42].
Size and number of tubers	It is claimed that the *S. andigenum* variety 'Tocana' crossed with domestic varieties produces seedlings with many large-sized tubers
High yield	Crosses of domestic potato and *S. andigenum* varieties, especially the variety *hederiforme*, through its forms '*tocanum*', *Usme*, and *tolucanum*; also the variety *quechuanum* [37]
Low yield	Hybrids with *S. andigenum* variety *ccompi* produce very low yields.
Number of tubers to the root: (*a*) Many tubers	Crosses between the domestic potato and the *S. andigenum* varieties *Pacus*, *quechuanum*, *tolucanum*, and *hederiforme*, all produce many tubers, often up to 30–40 to the root [37].
(*b*) Few tubers	Crosses with the *S. andigenum* variety ckello-huaccoto produce never more than 8 and those with Lisarca from 3–11 [37].
Long stems and many tubers	Is in general a character of the *S. andigenum* varieties and is dominant in F1 crosses with domestic varieties.
Uniformity of tuber-cluster	Hybrids of domestic potatoes with *S. andigenum* varieties Hederiforme type *Usme*, *quechuanum*, and *tocanum*, are said to produce good-sized and uniform tubers.

To meet Attacks of Disease and Pests

To combat insect pests	*S. Caldasii* (2*n* = 24) and *S. commersonii* are said to be definitely poisonous to insects [40, 43].
Resistance to the Colorado Beetle (*Leptinotarsa decemlineata*)	On *S. demissum* (2*n* = 72), *S. polyadenium* (2*n* = 24), *S. Jamesii* (2*n* = 24), and *S. Henryi* (2*n* = 24) the larvae fail to develop [44, 45, 46]. Some types of *S. acaule* are resistant to the larvae [47]. Certain hybrids of *S. acaule* and domestic potatoes are also resistant [44]. F1 of *S. chacoense* (2*n* = 24) × domestic varieties also show resistance [48]. Hybrids *S. demissum* × domestic European, some of *S. chacoense* by domestic, and all of *S. polyadenium* (2*n* = 24) × *S. Jamesii*, were highly resistant. In addition the seedlings of *S. Antipoviczii* (2*n* = 48) × *S. Emmae* (2*n* = 24), *S. commersonii* (2*n* = 36) × *S. Emmae* are said to be resistant. Some domestic varieties such as 'Erstling', i.e. Duke of York, Imperator, and Up-to-date, are less acceptable to the beetle than others [49].
Resistance to Eel Worm (*Heterodera schactii*)	Whilst no domestic variety has been found to be completely resistant, the varieties Epicure and Doon Star are much less heavily infected under like conditions than Majestic or Golden Wonder. The cysts, moreover, are smaller and develop fewer viable larvae [50].

Characters required	*Source*
Resistance to Leaf Hopper (*Empoasca fabae*)	*S. polyadenium* is immune [43]. *S. chacoense* (2*n* = 36), *S. commersonii*, and *S. caldasii* are highly resistant [43].
Resistance to Flea Beetle (*Epitrix Cucumeris*)	*S. polyadenium* is immune. *S. bulbocastanum* (2*n* = 24) is partially immune [43].
Resistance to Wart Disease (*Synchitrium endobioticum*)	There are many excellent domestic potatoes of all classes resistant to Wart Disease. See official lists of Ministry of Agriculture and National Institute of Agricultural Botany. Many of the wild species are resistant, as are also a large number of the varieties of *S. andigenum* [52].
Resistance to Blight (*Phytophthora infestans*)	*S. edinense* (2*n* = 60) [29] *S. Antipoviczii* (2*n* = 48) [53] *S. demissum* (*S. utile*) (2*n* = 72) [20, 54] *S. ajuscoense* (2*n* = 48) [56] *S. cardiophyllium* (2*n* = 36) [56] *S. bulbocastanum* (2*n* = 24) [56] *S. Aya Papa* [51, 57] = a misnomer for a hybrid of *S. demissum* × *S. tuberosum* [58] The varieties of *S. demissum* are the most important sources of resistance to the several biotypes of the fungus [59]. For best procedure in use of *S. demissum*, see Puškarev [60].
Resistance to Fusarium Wilt (*Fusarium oxysporum ; F. eumartii*)	In America several seedlings of domestic potato blood have given promising results. Of existing varieties Katahdin shows more resistance than do others [61].
Resistance to Scab (*Actinomyces scabies*)	*S. commersonii* [62] *S. chacoense* [62] *S. Jamesii* [62] A genetical analysis of Scab resistance in domestic potato varieties has been made [63]. Certain German domestic types show resistance: Richters Juliet; Erdgold; Hindenburg; Arnica [63, 64]. The German variety Carnea may be regarded as immune, and Akebia as fairly resistant [47].
Resistance to Ring Rot (*Phytomonas sepedonica*)	The varieties Friso and President are resistant [65]. Evidence is accumulating that seedlings of domestic breeds may be raised which are highly resistant [55].
Resistance to Virus Disease:	
Virus 'X'	Variety No. 41956 of U.S. Dept. of Agriculture is immune; it is derived from a native variety of Chiloe. Katahdin is somewhat resistant. Several varieties, notably Up-to-date, are protected from severe attack by natural infection with a symptomless strain. Craig's Defiance, Epicure, and King Edward are resistant to Virus 'X' in the field for the same reasons as those given below for Virus 'A'.
Virus 'A'	Craig's Defiance British Queen Up-to-date International Kidney } are highly susceptible to artificial infection but are immune in the field [68].

Characters required		*Source*
Virus 'A' (*cont.*)	Kerr's Pink, Sharpe's Express, Great Scot	are highly susceptible to artificial infection but are immune in the field [68]
Virus 'B' (Up-to-date Streak)	A large number of domestic, including Arran Pilot, Arran Victory, British Queen, Epicure, Golden Wonder, Kerr's Pink, and King Edward	behave as do those susceptible to Virus 'A' [68].
Virus 'C' (Di Vernon Streak)	Craig's Defiance, Arran Victory	behave as do those susceptible to Virus 'A' [68].

The resistance to the 'X' virus shown by variety No. 41956 is a true resistance and has a genetic background, based on the combined presence of two genes in an autotetraploid [66]; that of Katahdin, which is only partial, is not explained. The field immunity of the other varieties mentioned to the four viruses 'X', 'A', 'B', and 'C' is, in reality, due to an intense varietal susceptibility, which induces a local necrotic action at the point of inoculation which shuts off the virus and thus prevents a systemic infection. The reaction is based on four distinct and dominant genes, each of which controls the plant's reaction to one or other of the four viruses [67, 68].

Virus 'Y' — There is some reason to think that *S. Rybinii*, and possibly a few other wild species, may be resistant. K. O. Müller in Germany states that he has a Chilean variety which is immune [69].

Leaf Roll — No true resistance has been discovered; some varieties are more susceptible in the field than others. The varieties Flourball, Arran Banner, and Majestic are far less susceptible than Up-to-date, Signet, or President. Yet the yield of Up-to-date is less reduced by Leaf Roll than are those of less susceptible varieties [70]. The least susceptible is said to be Triumf [71].

It is possible that the reaction of varieties to the Leaf Roll virus may be due to several genes acting cumulatively. Only careful inbreeding would be likely to bring about an accumulation of such genes in one plant adequate for its use as a parental source of resistance.

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THE EFFICIENCY OF PROGENY-ROW-BREEDING IN COTTON IMPROVEMENT

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Introduction.—The evaluation of progress in plant-breeding work is difficult and it has not received the consideration it deserves. Assessments of progress have been made by Student [1] on selection for oil-content in maize, by Harland [2] on selection for lint-index in Montserrat Sea Island cotton, and by Hutchinson and Kubersingh [3] on the effect of selection in Malvi cotton. Theoretical aspects of the problem have been discussed by Fisher, Immer, and Tedin [4], Fairfield Smith [5], Hutchinson, Panse, and Govande [6], Hutchinson [7], and Panse [8]. Mason [9] has also discussed plant-breeding policy and has advocated considerable changes in current breeding methods.

This paper deals with the efficiency of the progeny-row technique in cotton breeding, and shows how plant-breeding data can be used to estimate the rate of improvement under selection.

History of the V 135 variety.—The breeding records of Sea Island superfine cotton in St. Vincent provide valuable information on the effect of a long period of self-fertilization and progeny-row selection on a comparatively uniform crop variety. The variety known as V 135 originated from a single-plant selection made by Harland in 1916 in a variable crop of Barbados Sea Island grown at Grand Sable Estate, St. Vincent. From 1916 to 1926 breeding work was in the hands of the Cotton Research Officer, and V 135 progeny rows were grown each year and self-pollinated. Selection was based on Harland's [10] analysis of yield in cotton, from which he concluded that boll characters, seed-cotton characters, and lint-length were those most likely to respond to selection.

From 1926 to 1930 the maintenance of the variety was in the hands of the Department of Agriculture, and the progeny rows were not always self-pollinated. In 1930 it was found that the V 135 breeding-stocks were seriously contaminated with 'ordinary' Sea Island, and a Cotton Research Officer was again appointed. The purity of the strain was re-established by rigorous selection. By 1932 the whole of the progeny-row material was descended from a single plant (V (30) 46) of the 1929–30 crop. A multiplication plot was also maintained, which was descended from two plants of the 1929–30 crop, V (30)13 and V (30)46. It was planted each year with seed from high-bolling selections from the previous multiplication plot, and surplus seed from the V (30)46 progeny rows. The proportion of V (30)13 descendants in it was therefore progressively reduced. Selections from the 1935–6 and 1936–7 multiplica-

tion plots were returned to the progeny rows, and provided some material (notably V (37)11) with rather higher lint-indices than the V (30)46 progenies.

From the 1937–8 season the progeny rows were grown in randomized block trials.

The Effect of Selection on V 135

In 1930 the newly appointed Cotton Research Officer based his re-selections in the contaminated superfine stock on lint-length. Lint-length determinations were made annually on the progeny-row material and provide a good index of the rate of purification of the variety. Data for the period 1930–7 are given in Table 1 (p. 142). Each observation represents a measurement on a single seed. Five measurements were made per plant. Data were recorded in this way in the early years, so single-seed measurements are used throughout for the sake of uniformity, although frequency arrays of single-plant means would be preferable. It will be seen that the effect of the first year's selection was to eliminate the whole of the lower tail of the frequency array. Thereafter very little change occurred, and there is no evidence that the upper limit of the distribution was raised by selection. As early as 1930 the Cotton Research Officer (S. H. Evelyn) concluded that the contamination was chiefly the result of mixing and not of hybridization, and the data support this view.

The selection pressure on any character may be measured by the difference between the mean values of the selected material and of the population from which it came. In progeny-row breeding the best progenies (i.e. highest mean values) are first selected, and then the best plants are chosen from the selected progenies, so that there are two selection pressures, measured by:

(1) The difference between the mean of selected progenies and the mean of all progenies (progeny-selection pressure).
(2) The difference in each progeny between the mean of the selected plants and the progeny mean (plant-selection pressure).

Mean values of all progenies, selected progenies, and selected plants, together with the selection pressures exercised on lint-length, lint-index, and seed-weight, are summarized for the period 1930–8 in Table 2. Lint-length is given throughout as maximum halo-length in mm., lint-index as mg. of lint per seed, and seed-weight as the weight of a single seed in mg.

In the first three seasons progeny selection was exercised on lint-length. There was also a considerable negative progeny selection on lint-index in the first year, and on seed-weight in the first two years. These negative selection pressures were not deliberately imposed, but resulted, in the first year at least, from the fact that the 'ordinary' material with which the superfine stock was contaminated had higher lint-indices and seed-weights than the superfine, and the selection of longer-linted progenies automatically reduced lint-index and seed-weight. The whole of the response occurred in the first year. It may be concluded that selection of good progenies in the first year effectually

TABLE 1. *Frequency Arrays of Lint-lengths of Single Seeds of V 135. Five seeds measured per plant*

	Measurements in millimetres																												
Year	*41*	*42*	*43*	*44*	*45*	*46*	*47*	*48*	*49*	*50*	*51*	*52*	*53*	*54*	*55*	*56*	*57*	*58*	*59*	*60*	*61*	*62*	*63*	*64*	*65*	*66*	*67*	*68*	*No.*	*Mean*
1929–30 .	1	..	1	3	5	9	6	4	15	18	22	37	36	66	87	69	**72**	63	23	12	3	2	1	..	..	..	..	..	555	54·66
1930–1 .	..	..	..	..	..	..	..	..	..	..	..	2	..	1	10	17	100	211	162	157	**101**	75	43	7	3	..	..	..	889	59·32
1931–2 .	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	11	45	83	95	78	51	**27**	6	2	..	..	..	..	400	59·20
1932–3 .	..	..	..	..	..	..	..	..	..	..	..	..	1	2	13	8	42	47	33	15	**18**	17	3	..	1	..	..	..	200	58·49
1933–4 .	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	95	108	105	125	111	**69**	24	11	1	..	..	..	655	59·60
1934–5 .	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	19	69	95	132	118	**139**	136	60	29	9	1	2	1	810	60·22
1935–6 .	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	3	39	50	**54**	36	49	29	13	2	..	..	..	..	275	59·53
1936–7 .	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	24	37	23	**26**	26	12	10	1	..	..	..	..	160	59·44

The group in which selections were made for the following year is printed in bold type.

TABLE 2. *Selection Pressure on V (30) 46*

TABLE 2. *Selection Pressure on V (30) 46*

Season		Mean values			Selection pressure						Remarks
					Lint-length		Lint-index		Seed-weight		
		Lint-length	Lint-index	Seed-weight	Progeny	Plant	Progeny	Plant	Progeny	Plant	
1929–30	All progenies	54·5	47·6	128·5	..	..	..	..	..	..	..
	Selected progenies	57·1	43·8	119·0	+2·6	..	−3·8	..	−9·5	..	..
	Selected plants	57·0	..	..	..	−0·1	..	..	..	..	..
1930–1	All progenies	59·4	40·8	122·5	..	..	..	..	..	..	..
	Selected progenies	60·3	40·6	125·7	+0·9	..	−0·2	..	+3·2	..	..
	Selected plants	61·0	39·0	117·9	..	+0·7	..	−1·6	..	−7·8	..
1931–2	All progenies	59·3	40·0	127·7	..	..	..	..	..	..	..
	Selected progenies	59·8	40·5	126·2	+0·5	..	+0·5	..	−1·5	..	..
	Selected plants	61·6	42·0	120·0	..	+1·8	..	+1·5	..	−6·2	..
1932–3	All progenies	58·4	36·3	117·0	..	..	..	..	..	..	Cotton stainer attack serious
	Selected progenies	58·6	37·1	117·7	+0·2	..	+0·8	..	+0·7	..	
	Selected plants	61·0	38·0	119·0	..	+2·4	..	+0·9	..	+1·3	
1933–4	All progenies	59·4	43·4	129·7	..	..	..	..	..	..	Sulphate of ammonia used for the first time
	Selected progenies	59·4	43·4	131·7	0·0	..	0·0	..	+2·0	..	
	Selected plants	62·0	45·0	132·0	..	+2·6	..	+1·6	..	+0·3	
1934–5	All progenies	60·5	42·5	125·5	..	..	..	..	..	..	..
	Selected progenies	60·4	42·2	124·7	−0·1	..	−0·3	..	−0·8	..	..
	Selected plants	61·4	45·0	134·0	..	+1·0	..	+2·8	..	+9·3	..
1935–6	All progenies	59·8	43·5	133·9	..	..	..	..	..	..	..
	Selected progenies	59·3	44·6	134·8	−0·5	..	+1·1	..	+0·9	..	..
	Selected plants	58·8	50·0	142·0	..	−0·5	..	+5·4	..	+7·2	..
1936–7	All progenies	59·4	44·6	137·7	..	..	..	..	..	..	..
	Selected progenies	58·1	45·2	133·0	−1·3	..	+0·6	..	−4·7	..	..
	Selected plants	60·4	51·0	144·0	..	+2·3	..	+5·8	..	+11·0	..
1937–8	All progenies	58·4	43·4	131·1	..	..	..	..	..	..	..
Total selection pressure		..	..	..	+2·3	+10·2	−1·3	+16·4	−9·7	+15·1	..
Total selection effect		+3·9	−4·2	+2·6	..	..	..	..	..	..	..

restored the integrity of the superfine type. Mean values for seed-weight and lint-index were greatly affected by environmental factors. In 1932–3 both were lowered by an early and heavy infestation of cotton stainers. In 1933 manurial policy was changed. In that and subsequent years substantial dressings of sulphate of ammonia were applied, and lint-index and seed-weight rose in response. Deliberate selection for high lint-index and seed-weight was begun in 1934–5, but was practically confined to plant-selection. As might have been expected from plant-selection in very uniform material, there was little response, and in 1937–8 the means of all progenies for lint-index and seed-weight were little different from those of 1933–4.

In the replicated progeny-row trial in 1937–8 differences in lint-length and seed-weight between progenies descended from V (30) 46 were insignificant. Differences in lint-index were regarded as significant, but were not confirmed by the small-bulks trial of the same material in the following season. Nine re-selections from the multiplication plot were also included in the 1937–8 trial. Most of them were indistinguishable from the V (30) 46 progenies, as was to be expected, but a few (notably V (37) 11) had significantly higher lint-indices and shorter lint. V (37) 11 was carried on, and in the following year gave one progeny that was significantly lower than the rest in lint-index. After the low segregate had been discarded, no further evidence of genetic variance in V (37) 11 was obtained. The new V 135 material, therefore, consists of two practically homozygous sub-strains (V (30) 46 and V (37) 11) differing slightly in lint-index and lint-length.

The best estimate of the effect of selection in the V 135 stock would be a direct comparison of the original material with the new V 135 of the current breeding-stocks. Although the original material is not available, a strain representative of the breeding-stocks of 1920 has been preserved. Its history is as follows:

In 1920 Harland left St. Vincent and took seed of V 135 with him. It was grown and self-pollinated for three generations in a greenhouse in Manchester, and then taken to Trinidad, where it was grown and selfed for several generations more (Harland, personal communication). About 1928 a clone (Type 18) was established by grafting, and later (1937–8) a progeny row from the clone was grown in St. Vincent. Selections from this progeny provided material of the early V 135 for comparison with modern selections in 1938–9.

It is important to decide how far Type 18 can be regarded as representative of the strain Harland left in St. Vincent in 1920. No conscious selection has been exercised on it since then, but it might differ from its prototype in consequence either of the choice of an off-type parent in the first place, or of chance divergence in later generations. The variety was uniform in 1920, so that the chance of a very divergent type providing the foundation stock of Type 18 is small. Less than 10 generations are involved, so that change by random change in gene-frequencies could scarcely be appreciable. Mason [9] suggested that variation might be increased by the operation of functional heredity through acclimatization effects. Such evidence as is available on the effect of acclimatization on

cotton varieties indicates that no change is induced in the genotype. Evelyn (unpublished report) sent V 135 seed to Tenerife. The Tenerife-grown progeny was 5–6 weeks later in flowering and about 8 weeks later in maturing the crop than St. Vincent V 135, and the seed-cotton produced had a 33 per cent. lower lint-index and 13 per cent. lower lint-length. Selfed seed from Tenerife grown again in St. Vincent, however, produced plants that were normal V 135 in all respects. In another experiment, C 402, a Cawnpore *desi* cotton was grown and selfed for several generations in Trinidad by the senior author, and then grown at Indore, Central India, in a replicated progeny-row trial with C 402 direct from Cawnpore and C 402 grown for 4 generations at Indore. There were no differences between the three types either in mean values or in progeny variation. Considering, therefore, the comparative uniformity of the V 135 stock, the absence of selection, and the short period over which chance divergence could have occurred, it is safe to conclude that Type 18 does not differ markedly from the early V 135 type.

In the 1938–9 season a replicated progeny-row trial was carried out with 10 progeny rows of the new V 135, and 10 of Type 18. There were 10 randomized blocks, and each progeny plot contained 5 plants. The main strains were arranged in a 'compact family block' layout [11]. For the main-variety comparison, therefore, there were 10 replicates of 50 plants each. A comprehensive study of the two main strains was made, and mean values for 12 characters are given in Table 3. With them are tabulated the mean squares for differences between progenies of the same strain to facilitate comparison of within-strain variation. New V 135 was later in forming the first fruiting branch and the first flower, and taller at maturity. It produced slightly fewer bolls, but they were significantly larger. Lint-index and seed-weight were higher but ginning percentage was lower, and the increment in lint-yield over Type 18 was consequently not quite as great as the increment in seed-cotton yield. New V 135 was considerably superior in length. Samples of bulks of Type 18 and new V 135 from the 1939–40 crop were submitted to the Shirley Institute for spinning tests. They did not differ in fineness, but new V 135 was about 12 per cent. longer and gave about 10 per cent. stronger yarns.

In Table 3 for each strain is given *P*, the probability that the observed differences between progenies of the same strain might occur by chance. It will be seen that there were no significant differences between progenies in either strain in the first six characters, all of which, except node number, are subject to great environmental variation. In seed-cotton characters the significant differences between progenies of new V 135 were due to differences between V (30) 46 and V (37) 11. Variation between progenies was from $1\frac{1}{2}$ to 7 times as great in Type 18 as in new V 135.

The Type 18 progenies were only the second generation from a single plant, whereas in new V 135 the sub-strains were of distinct ancestry for several generations. Among the six V (37) 11 progenies, which were also only the second generation from a single plant, there were differences just reaching the level of significance in lint-length and lint-index only.

TABLE 3. *Comparison of New V 135 and Type 18 in 1938–9*

Character	*Type 18*			*New V 135*			*Strain difference per cent.*	*P (strains)*
	Mean	*Mean square between progenies*	*P (Progenies)*	*Mean*	*Mean square between progenies*	*P (Progenies)*		
Node number (of first fruiting branch)	9·8	0·31	large	11·8	0·51	large	18·5	‡
Days to first flower	69·5	2·75	large	71·8	7·04	large	3·3	†
Height at maturity (cm.)	129·9	82·91	large	146·1	98·56	large	11·8	†
Bolls per plant	57·2	129·89	large	53·7	92·67	large	−6·3	large
Seed-cotton per plant (gm.)	117·7	614·18	large	135·9	738·81	large	14·4	†
Lint per plant (gm.)	30·3	45·32	large	34·4	52·07	large	12·7	nearly *
Seed-cotton per boll (gm.)	2·05	0·0495	‡	2·53	0·0308	large	21·0	‡
Lint per boll (gm.)	0·53	0·0074	‡	0·64	0·0021	large	18·8	‡
Lint-length (mm.)	57·3	7·38	‡	60·7	1·03	†	5·8	‡
Lint-index (mg. per seed)	38·8	17·94	‡	39·9	4·50	†	2·8	‡
Seed-weight (mg. per seed)	112·3	72·11	‡	117·7	17·57	*	4·7	‡
Ginning percentage	25·7	5·09	‡	25·3	1·12	†	−1·2	†

* P between progenies $< 0{\cdot}05$. † P between progenies $< 0{\cdot}01$. ‡ P between progenies $< 0{\cdot}001$.

Note. The lint-index and seed-weight figures in Table 2 were calculated from selected samples of the single-plant produce. Those in Table 3 were calculated from the total seed-cotton and total lint of the plant and the seed-weight of carefully taken random samples of the seed. They are about 10 per cent. lower than comparable figures from selected samples.

New V 135 is clearly a considerably better strain than Type 18. During the period for which detailed records are available, however (1929–30 to 1938–9 seasons), improvement was confined to the elimination of inferior material in the first year and the isolation of the higher lint-index sub-strain, V (37) 11, in 1936–7. Since there appears to be practically no genetic variance remaining within new V 135 strains, no further response to selection is to be expected.

The genetic variance in Type 18 may be regarded as a minimum estimate of that in the V 135 stock of 1920, since factors for which the Type-18 clone was homozygous may well have been represented by their alleles in other plants in the original material. Even with the variability demonstrated in Type 18 it is clear that the old V 135 would respond considerably to selection in seed-cotton characters. Though there was no demonstrable genetic variance in total yield of seed-cotton or of lint, the differences between the old and new V 135 in these characters were no doubt the direct consequences of selection in seed-cotton and lint per boll, in which, with a low environmental variance, it was possible to show that the genetic variance was considerable. The reduction in bolls per plant, though not statistically significant, was not unexpected, since an increase in boll-size will increase the drain on the available food supplies, and it is likely that boll-number will suffer to some extent in consequence. Changes in node-number (and consequently in earliness) and in height at maturity may be ascribed to the selection of genes not carried by Type 18.

The Effect of Selection on U 4

The selections from which the new V 135 is descended were genetically uniform, and the strain has been bred for uniformity to satisfy the seed-supply requirements of the growers of superfine. Its breeding behaviour may be contrasted with that of U 4, the South African jassid-resistant Upland cotton. An account of the origin and early breeding history of U 4 is given by Parnell [12]. It was a single-plant selection from a variable bulk known as 'Uganda', made in the 1924–5 season, and Parnell states that 'the first progeny row was by no means uniform, but showed variation, obviously due to segregation, in various characters'. The breeding policy adopted tended to conserve this genetic variability. The single-plant selections made 'were all promising economic types, possessing a sum-total of characters likely to make them useful in actual practice, but they were chosen to cover a wide range in habit, duration etc.' Further, '. . . a wide range of types was taken in making selections, the policy being to narrow these down gradually, after experience with them in different conditions, rather than to discard all but a few of the best in any one season' [12]. Lastly, 'Special Bulks' were made and maintained from the first U 4 progeny, and from later promising selections, and these provided both reservoirs of variability for subsequent re-selection, and material representative of the stages of the selection process which could be compared in later years.

Special Bulks of U 4 selections made over a period of twelve years were included in trials carried out by Macdonald, Fielding, and Ruston

[13, 14] in the 1938–9 and 1939–40 seasons. Their data (rearranged for case of comparison) are quoted in Table 4. The original V 4 was so good that all other material was discarded from the breeding plots by 1929 [12], and the products of progeny selection in it so much better, that selection in U 4 hybrids, which has been carried out over most of the period, has not yet produced a strain to compete with them. The contrast between the stability of V 135 and the striking progressive change in U 4, illustrated in Table 4, is an excellent demonstration of the fundamental importance of genetic variability in determining the capacity to respond to selection.

TABLE 4. *Yields of U 4 Selections of Different Ages, expressed as Percentages of the Yield of U 4/4/052/5143*

Strain	*Year of selection*	*Yield as a percentage of 5143*		*Date of putting into general cultivation*
		1938–9 trials	*1939–40 trials*	
U 4 Bulk	1925	..	68	1929–30
U 4/4	..	..	81	..
U 4/4/052	1930	94	85	1935–6
U 4/4/052/5143	1935	100	100	1939–40
U 4/4/052/5143/6128, and 6130 .	1936	108	101	..
Ten 1937 selections . . .	1937	119	..	..
$P = 0{\cdot}05$	..	..	5·7	..

The data given in Table 4 refer to Barberton selections only. The early U 4 bulk was such a great improvement on all other available varieties that it rapidly became the standard variety and breeding stock in the Rhodesias and Nyasaland. Some of the first selections from it were distributed in parts of Tanganyika, and provided successful breeding material for part of Uganda. Recent, highly successful selections, however, do not appear to have the wide range of adaptability of the early stocks, and it appears that the selection exercised has been largely in the direction of closer adaptation to the local environment. The extent of this local adaptation is well illustrated by comparisons of the Barberton material of 052 descent with Southern Rhodesian material of U 4/64 ancestry. Peat and Prentice [15] reported that at Gatooma (S. Rhodesia) in the 1937–8 season the Barberton strains 052, 5143, and 5149 'were striking in the early part of the season, and grew out better than the material around, possibly too well for a droughty season: they were "sticky" in their finish, and appeared unhappy in their final cropping. They yielded better than their appearance had indicated, but lower than the U 4/64 material around.' Similar comments were made in 1936–7 and 1938–9. Macdonald, Fielding, and Ruston [13] reported on a trial of 4 Gatooma strains and 5 Barberton strains carried out at Barberton in 1939–40. The mean yield of seed-cotton per acre of the 4 Gatooma strains was 741 lb., and of the 5 Barberton strains, 1034 lb., and the authors comment: 'As was to be expected, the Barberton strains were more at home than those from Gatooma, giving better general develop-

ment and being much less quickly affected by the drought.' The intimate nature of the relation between genotype and environment involved in local adaptation is well brought out by the fact that each group of strains proved the more drought-resistant of the two on its home station.

Discussion

The breeding history of V 135.—Before discussing the bearing of the V 135 work on the improvement of breeding technique, it must be pointed out that the improvement of the superfine strain was never its chief object. The provision of ample planting seed of the highest possible purity is vital to the success of the Sea Island cotton industry, and the seed-supply is therefore the chief care of the Cotton Research Officer. It is good evidence of the success of the breeding work that the replicated progeny-row trials show that the genetic variability of new V 135 has been reduced almost to vanishing point.

It is evident from the data given in Table 3 that new V 135 represents a handsome all-round improvement over Type 18. The analysis of its selection history shows, however, that no improvement, apart from a small increase in lint-index, was made after the selection of the two 1929–30 plants (V (30) 13 and V (30) 46) from which the new V 135 stock is descended. Since manuring practice and methods of sampling for seed-cotton characters were similar in 1922 and 1931, it is worth comparing the mean values of the V (30) 13 and V (30) 46 progenies in 1930–1 with the values for V 135 given by Burd (Prog. Rept. 1923–4).

Character	*Seed-cotton per boll gm.*	*Lint per boll gm.*	*Lint-length mm.*	*Lint-index mg. per seed*	*Seed-weight mg. per seed*	*Ginning per-centage*
1922–4 . .	2·90	0·71	57·1	38	117	24·5
1930–1 . .	3·25	0·86	59·1	45	127	26·4
Percentage diff. .	+12·1	+21·1	+3·5	+18·4	+8·6	+7·8

The differences in favour of the 1930–1 progenies support the evidence adduced from the 1938–9 replicated trial to show that practically the whole of the change from Type 18 to New V 135 occurred prior to 1931.

The superiority of V (30) 13 and V (30) 46 over the earlier V 135 cannot be ascribed to direct selection on measured characters, since when they were selected the first consideration was the re-establishment of the superfine type, and for this lint-length was the only measured character used. As Hutchinson and Kubersingh [3] found when discussing the improvement of Malvi cotton, the conclusion is unavoidable that the superiority of the selected strain 'must be ascribed to that indefinable judgment of unmeasured characters, the necessity for which makes plant-breeding as much an art as a science'.

The genetic basis of progeny selection.—The conclusion that plant-breeding success has in the past resulted chiefly from the exercise of the breeder's art, and not from the careful analysis of numerical data, led Mason [9] to suggest that the chance of obtaining an improved crop variety would be greater if less attention were paid to the accumulation

of accurate statistical knowledge of the breeding material and more effort devoted to the exercise of the breeder's art. Mason contrasted the large successes of 'primary selection' (single-plant selection in large field populations) with the small gains commonly achieved by 'secondary selection', which he defined as single-plant selection in progeny rows. Though Mason's contrast is real, it results from a difference in the material rather than in the technique of selection. Given a highly variable unselected crop population it is likely that the first batch of primary selections will be a very considerable improvement on the parent bulk. On distribution these will replace the old population and further improvement will be more difficult to achieve, firstly because the available genetic variability will be less, and secondly because the general level of performance will be higher. It is to be expected therefore that the rate of improvement will decrease as the extent of the improvement increases. As the contrast between the breeding behaviour of V 135 and U 4 shows, the fundamental factor concerned is the genetic variability of the material, and not the breeding system adopted.

The comparison of single-plant selection in large populations with single-plant selection in progeny rows obscures the chief function of progeny-row breeding, which is to minimize the environmental fluctuations while maintaining the genetic contrasts. This is done by transferring selection from the single plant to the progeny mean. Since the value of selection on progeny means seems at times to be overlooked,* it is worth considering in some detail the distribution of genetic and environmental variance within and between progeny rows.

Let

V_G be the genetic variance between plants,

V_E be the environmental variance between plants,

m be the number of plants per progeny,

$d_1, d_2, \ldots, d_r$ be half the difference between the homozygotes for the factors $D_1, D_2, \ldots, D_r$,

$h_1, h_2, \ldots, h_r$ be the deviation of the heterozygote from the mean of the homozygotes for the same factors, and

E be the efficiency factor $\frac{V_G}{V_E}$.

The greater the ratio of V_G to V_E, the greater the efficiency of selection. One of the chief effects of selection, however, is to reduce V_G, so that selection will become less efficient as the breeding work proceeds unless means of reducing V_E are available.

It has been shown [4] that in the progeny of a single plant, each factor for which it is heterozygous will contribute to V_G

$$\tfrac{1}{4}(2d^2+h^2).$$

Then in the progeny of a plant heterozygous for $D_1, D_2, \ldots, D_r$

$$V_G = \tfrac{1}{4}S_r^1(2d^2+h^2),\dagger$$

* Jameson [16], for instance, criticized the replicated progeny-row technique thus: 'The layout was successful as a variety trial but it did not lend itself to successful single-plant selection. . . . ' It was, of course, never intended to facilitate single-plant selection.

† This will be true if the effects of $D_1, D_2, \ldots, D_r$ are additive. That the effects of a

and the efficiency factor will be

$$E = \frac{\frac{1}{4}S_r^1(2d^2+h^2)}{V_E}.$$

With mass breeding the magnitude of V_G in later generations will depend on the selection exercised and the rate at which the proportion of heterozygotes is reduced by inbreeding, but assuming no selection and random recombination of genes, the upper limit will be

$$V_G = S_r^1(d^2),$$

when the population consists of equal numbers of + and − homozygotes in each factor.

The efficiency will then be

$$E = \frac{S_r^1(d^2)}{V_E}.$$

If in the same material single-plant progenies are kept separate, the genetic variance between second-generation progeny means assuming no selection [4] will be $\frac{1}{4}S_r^1(2d^2+\frac{1}{4}h^2)$.

The environmental variance between progeny means, on the other hand, will be

$$\frac{V_E}{m},$$

and the efficiency factor will be

$$E = \frac{\frac{1}{4}mS_r^1(2d^2+\frac{1}{4}h^2)}{V_E},$$

which will be approximately m times that of selection in a single plant progeny. In later generations, as the proportion of segregating progenies is reduced by selfing, in the absence of selection the genetic variance between progeny means will approach the same limiting value, $S_r^1(d^2)$. Then the efficiency factor for selection on progeny means will be

$$E = \frac{mS_r^1(d^2)}{V_E},$$

which is m times the efficiency factor of primary selection in a similar population. Selection on the means of progenies of m plants each, therefore, is approximately m times as efficient as primary selection in the same material, irrespective of its genetic constitution.

At first sight it would appear that the advantage of selection on progeny means will be counterbalanced by the reduction in the amount of material in which selection can be exercised. If facilities permit a crop of k plants, there will be only k/m progeny means among which to select, as against k single plants. It must be remembered, however, that single-plant selection can still be exercised within the best progenies, so that by

considerable number of genes of small individual effect will be strictly additive is unlikely, but the nature of the gene interaction will affect the rate of decay of the variance, and not the comparative magnitude of the variances in mass populations and progeny rows of the same material. For the purpose of the argument, therefore, S_r^1 means the cumulative effect of genes D_1 to D_r without specifying the nature of the interactions between them.

the maintenance of separate progenies the breeder has the advantage of progeny selection in addition to (and not instead of) single-plant selection. Where a limited number of plants can be grown, the optimum progeny-size requires careful consideration. Variable material must be sampled extensively if its potentialities are to be exploited adequately and a large number of small progenies will be more useful than fewer large ones. As the breeding stock becomes more homogeneous, the differences to be selected become smaller and progeny-size must be increased if they are to be detected with confidence.

Since in Mason's [9] definition the essential component of progeny-row selection—selection on progeny means—is omitted, it seems preferable to revert to the older terms, mass selection for single-plant selection in large mixed populations, and progeny selection for selection based on progeny means in pedigree material.

The design of a breeding project.—A sound breeding programme should meet three requirements:

1. The objective should be clearly defined.
2. The selection exercised and the improvement gained should be measured.
3. The breeding material should be made to yield an estimate of the capacity for further improvement.

(1) The need for a clear aim should be obvious, but it is not uncommon for selection to be carried out with no better definition of its objective than that an improvement in any character would be welcome. The proper definition of a breeding aim demands careful consideration of the consumer's needs, the agricultural conditions, and the available genetic variability. In superfine Sea Island cotton consumers' requirements rule out any change in quality, since anything longer or finer would be beyond the capacity of existing machinery, and anything inferior would not compete in the superfine market. Study of the agricultural situation in St. Vincent revealed a pressing need for a variety better suited to the poorer cotton lands, and a survey of the variability in the Sea Island group indicated that such a variety might be obtained by selection in a hybrid between V 135 and the MS 1 variety from Montserrat. The future breeding programme is therefore limited to the specific problem of breeding a superfine cotton with a better yielding capacity on poor land.

(2) The importance of measuring the selection exercised has been shown by Hutchinson and Kubersingh's [3] examination of the Malvi selection work as well as by the examination of the V 135 breeding in this paper. In both cases the magnitude of the selection exercised was considerably less than was believed, and the portion of it exercised between progeny means was unduly small. The measurement of selection pressure is not difficult, and has been discussed above in connexion with the data given in Table 2. Estimating the response to selection is not difficult, and can be done by including unselected material as a control in breeding tests. This is not usually possible in progeny-row trials since, if the genetic variance is at all large, a considerable number of progenies will be required to sample adequately the unselected material. Controls can easily be included in a trial of small second-generation

bulks, however, and in most breeding schemes with which seed multiplication and distribution are associated, the main bulk stock for distribution represents the breeding material of three or four generations earlier, and provides a very suitable basis for comparison. The value of such comparisons of stages in the breeding process is illustrated by the data quoted above from the comparison of U 4 Special Bulks.

(3) It is evident that, had a satisfactory method of estimating the capacity for further improvement been available, V 135 would have been put on a maintenance basis by about 1933–4 and attention concentrated almost entirely on more variable hybrid stocks. What the breeder requires is evidence in each generation that the breeding material still contains genetic differences large enough to be detected and isolated by selection. It is here that the chief advantage of replication in progeny-row breeding is obtained. Where variability is high and responses to selection are obvious the labour involved in the statistical reduction of data from replicated trials is not worth while. When the major differences have been exploited, further progress depends on the steady accumulation of small advances. Then the estimate of the magnitude of the environmental variance provided by data from a replicated trial makes it possible to decide whether the differences between progeny means are significantly greater than can be accounted for by fluctuations of environmental origin. Where no significant differences occur between progenies it may be safely assumed that the genetic variance is small relative to the environmental variance of the progeny means, and in default of still further refinements in breeding technique, continuation of selection will not yield any appreciable return.

The conservation of variability is a matter deserving of much closer attention than it commonly gets from the plant-breeder. In Sea Island breeding uniformity has always been demanded. In the U 4 work the value of variability was fully recognized from the beginning, and variability has been successfully maintained in the breeding stocks. The resulting continued capacity to respond to selection is amply demonstrated by the data in Table 4.

In conclusion it may be said that the best opening for increasing the efficiency of plant-breeding technique lies in the refinement of the progeny-row system. In a well-designed breeding project it can be made to yield information on the selection exercised, the improvement gained, and the possibility of further response.

Summary

1. The breeding history of the superfine Sea Island cotton V 135 is described, and the achievements of selection evaluated from a comparison between modern strains of the variety and a representative of the 1920 stock.

2. It is shown that the modern strains carry no appreciable genetic variance and, as would be expected, there has been no response to selection in them. Improvement was considerable in the earlier years, and evidence is presented to show that at that time there was considerable genetic variance in the variety.

3. The response to selection attainable in pedigree material of suitable genetic constitution is illustrated by data on the breeding history of U 4 cotton, and it is concluded that all available information supports the view that the capacity to respond to selection is a function of the genetic variance of the material.

4. The advantage of progeny-row breeding over mass selection is considered. Its chief merit is that the ratio of the genetic to the environmental variance is very much greater between progeny means than between plants of a mixed population of the same genetic constitution. Selection on progeny means is m times as efficient as mass selection in the same material where m is the number of plants per progeny.

5. Factors governing the efficiency of a breeding programme are considered, and it is shown that a well-designed progeny-row breeding programme will yield the information the breeder requires.

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The extent to which we have drawn on the published reports of the U 4 breeding work will be evident from the references. We wish to acknowledge also the debt we owe to those working on U 4, particularly Mr. F. R. Parnell, who have discussed their breeding methods with us in correspondence.

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THE BURIED VIABLE-SEED CONTENT OF A MIDLAND CALCAREOUS CLAY SOIL

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THE investigation of the buried viable-seed content of soils beneath pastures was first undertaken at the Welsh Plant Breeding Station in 1929. Work on this buried-seed problem had been conducted by Brenchley [1] and by Brenchley and Warington [2 and 3] at Rothamsted, and the technique adopted at Aberystwyth was very similar to that used by these investigators. The field of study, however, differed in that in the Aberystwyth area the investigations have been chiefly concerned with the soils beneath lowland and hill grassland. The first experiment [4], which was very detailed with regard to the numbers of viable seeds of species at various depths below the surface, showed that the results of such an investigation could be of immediate practical value as well as providing an ecological study in the surface-vegetation and buried viable seeds of grassland types. The data indicated, in fact, that prognostications could be made as to the volunteer-plant growth following cultural operations of these particular pastures. It thus became apparent that a method of soil sampling which would enable numerous fields and areas to be dealt with in a survey-type of investigation, and the preliminary results obtained within three to four months, would provide material of considerable practical significance; for by this means the cultivations and cropping of newly acquired farms could be planned in view of the known quantities of the viable seeds of certain weeds in particular fields, or, on the other hand, advantage could be taken of the presence in the soil of the seeds of valuable grasses and clovers which would contribute to the formation of a new sward.

A survey of buried viable seeds was conducted on the fields and hill areas of the Cahn Hill Improvement Scheme, when those lands were taken over in 1933, by the use of a borer for taking the soil samples instead of the more elaborate method needed in the first experiment for obtaining detailed results at depth [4]. The latter method of sampling, used on the numerous sward types under cultivated and natural conditions of the Cahn Hill Improvement Scheme, as well as on the arable fields, provided information which was used in the practical way mentioned above; whilst an extension of the period of investigation into a second year, until no more seedlings appeared from the soils, provided more complete data in these respects, and also a comprehensive ecological study of the flora from buried viable seed of the numerous habitats [5].

When the Grassland Improvement Station was started at Stratford-on-Avon a similar survey was carried out under the directorship of Sir R. G. Stapledon. Each field of the Drayton and Dodwell farms of the station was sampled and the soils taken to Aberystwyth for investi-

gation. The soils were put out for study at the end of April 1940, and the results of the first germinating period, up to September of that year, have been given in an account of the early work of the Grassland Improvement Station at Stratford-on-Avon [6], to which references will be made in the present report. The soils were kept under investigation for two years from the commencement of the experiment, at the end of which extremely few germinations were observed. The data from these Warwickshire fields form the subject of this paper.

Experimental method.—The type of herbage on the Drayton and Dodwell fields and the condition of the farms in general have been described by Stapledon [6]. At Drayton the grass fields consisted of old tumble-down swards and poor leys, and the arable land was foul; there was much bramble and thorn, and the watercourses were clogged. At Dodwell most of the fields were in poor grass, much of it in high ridge and furrow, and many fields needed drainage. Tor grass was frequent in the pastures of both farms. There were few arable fields at Dodwell, and these were of a poor yielding quality. In his detailed description of the soils Mr. Morley Davies [6] of the Harper Adams Agricultural College states that 'the area occupied by the two farms lies on the Lower Lias formation, which extends over a considerable part of the surrounding district. It consists of an alternation of thin beds of limestone and clays.'

The methods of sampling in the field for determining the buried-seed content and the subsequent treatment of the soils in the greenhouse have been recorded elsewhere [4, 5]. It may, however, be mentioned here that in the survey-method a definite number of soil borings 7 in. in depth are taken from each field, after first removing a small disk of turf in the case of grassland, the under-soil from which is kept in addition to the boring. In the greenhouse the soils are placed in shallow boxes over a layer of silver sand and kept in a condition favourable to seed-germination and subsequent growth of seedlings. The soils are stirred after the removal of crops of seedlings.

The data are presented here so as to give the results from each farm separately. Those for the permanent pasture fields are given in a frequency table, as they were too numerous to give individually, but the data from the arable and other classes of fields have been entered separately for each one. Five extra fields at Drayton were taken over at a later date than the main farm, and the data from these cover a period of 14 months instead of 2 years, as is the case of the main survey. These data are given in Table 3 (p. 160). In the frequency section of Table 1 four groups with a class interval of 2·5 millions have been taken, the first group containing under 0·5 million and the last group over 5·5 million viable seeds. It was found that this range covered the seedling numbers for the majority of the species, but particulars for two species which gave very large numbers of seedlings have been given separately in a footnote.

The scientific names of the species have been used in the tabulation, but in the text these have been supplemented with the common names which have usually been given once only. An Appendix is added containing the common names of other species not mentioned in the text.

TABLE 1. *Number of Fields in which Each Species occurred, Maximum Number of Viable Seeds (in Millions per Acre to a Depth of 7 in.), and Grouped Frequencies of Other Quantities in 11 Permanent Pasture Fields in Drayton (Nos. 3, 5, 6, 7, 8, 10, 11, 14, 16, 18, 19) and 12 in Dodwell (Nos. 20, 'by 20', 21, 22, 25, 26, 27, 29, 30, 31, 33, 34)*

Species	Drayton						Dodwell					
			Group						Group			
	No. of fields	Maximum quantity	Under 0·5	0·5–3·0	3·1–5·5	Over 5·5	No. of fields	Maximum quantity	Under 0·5	0·5–3·0	3·1–5·5	Over 5·5
Miscellaneous species:												
Achillea millefolium Linn.	..	..	..	..	..	..	2	0·41	2	..	..	..
Aethusa cynapium Linn.	8	1·84	2	6	..	..	5	1·84	2	3	..	..
Agrimonia cupatoria Linn.	..	..	..	..	..	..	1	0·41	1	..	..	..
Allium vineale Linn.	2	1·02	..	2	..	..	1	0·20	1	..	..	..
Anagallis arvensis Linn.	10	7·95	1	4	3	2	5	6·32	2	2	..	1
A. caerulea Sm.	1	0·41	1	..	..	..	..	..	..	..	..	..
A. tenella Linn.	..	..	..	..	..	..	1	0·41	1	..	..	..
Bartsia odontites Huds.	7	2·44	4	3	..	..	1	0·20	1	..	..	..
Bellis perennis Linn.	10	4·70	..	7	1	2	10	6·93	3	6	..	1
Brassica campestris Linn.	..	..	..	..	..	..	1	0·41	1	..	..	..
B. sinapis Vis.	7	3·46	3	2	2	..	7	1·63	3	4	..	..
Capsella bursa-pastoris Medik.	1	0·20	1	..	..	..	..	..	..	..	..	..
Cardamine amara Linn.	1	0·82	..	1	..	..	..	..	..	..	..	..
C. hirsuta Linn.	6	0·61	4	2	..	..	6	0·61	5	1	..	..
Carduus arvensis Robs.	8	2·86	4	4	..	..	4	0·20	4	..	..	..
C. palustris Linn.	2	0·61	1	1	..	..	2	0·61	1	1	..	..
Carex species	5	6·93	1	3	..	1	11	2·65	2	9	..	..
Centaurea nigra Linn.	1	0·41	1	..	..	..	..	..	..	..	..	..
Cerastium vulgatum Linn.	9	2·65	..	9	..	..	11	7·75	..	7	3	1
Chenopodium album Linn.	2	0·20	2	..	..	..	2	0·41	2	..	..	..
C. glaucum Linn.	2	1·43	1	1	..	..	..	..	..	..	..	..
Chrysanthemum leucanthemum Linn.	2	1·63	..	2	..	..	8	2·65	2	6	..	..
Conopodium denudatum Koch.	1	0·20	1	..	..	..	..	..	..	..	..	..
Crepis paludosa Moench.	1	0·20	1	..	..	..	..	..	..	..	..	..
Daucus carota Linn.	2	4·48	1	..	1	..	..	..	..	..	..	..
Epilobium montanum Linn.	..	..	..	..	..	..	1	0·20	1	..	..	..
E. palustre Linn.	..	..	..	..	..	..	2	0·41	2	..	..	..
Euphorbia exigua Linn.	6	2·44	2	4	..	..	3	1·84	..	3	..	..
Galium palustre Linn.	..	..	..	..	..	..	3	0·82	1	2	..	..
G. verum Linn.	..	..	..	..	..	..	1	0·41	1	..	..	..
Geranium dissectum Linn.	1	0·82	..	1	..	..	..	..	..	..	..	..
G. molle Linn.	9	1·63	2	7	..	..	..	..	..	..	..	..
Hieracium pilosella Linn.	1	0·20	1	..	..	..	..	..	..	..	..	..
Hydrocotyle vulgaris Linn.	..	..	..	..	..	..	1	0·20	1	..	..	..
Hypericum humifusum Linn.	9	8·98	4	2	1	2	8	6·32	1	5	1	1
H. perforatum Linn.	7	5·10	3	2	2	..	5	0·82	3	2	..	..
Hypochoeris radicata Linn.	2	0·20	2	..	..	..	1	0·20	1	..	..	..
Jasione montana Linn.	1	0·61	..	1	..	..	..	..	..	..	..	..
Juncus articulatus Linn.	2	0·20	2	..	..	..	7	0·82	6	1	..	..
J. bufonius Linn.	..	..	..	..	..	..	2	0·82	1	1	..	..
J. communis Mey.	5	0·41	5	..	..	..	9	4·08	5	3	1	..
Leontodon hispidum Linn.	2	0·41	2	..	..	..	2	0·20	2	..	..	..
Linaria elatine Mill.	2	0·41	2	..	..	..	..	..	..	..	..	..
L. spuria Mill.	4	1·43	3	1	..	..	2	0·41	2	..	..	..
Linum catharticum Linn.	7	2·04	4	3	..	..	4	1·02	2	2	..	..
Luzula campestris D.C.	1	0·20	1	..	..	..	5	0·41	5	..	..	..
Myosotis arvensis Hill.	2	0·20	2	..	..	..	1	0·20	1	..	..	..
Onopordon acanthium Linn.	4	0·82	3	1	..	..	..	..	..	..	..	..
Pedicularis sylvatica Linn.	1	0·20	1	..	..	..	..	..	..	..	..	..
Plantago lanceolata Linn.	7	1·63	3	4	..	..	2	0·61	1	1	..	..
P. major Linn.	6	1·63	3	3	..	..	5	1·22	4	1	..	..
P. media Linn.	10	29·27	1	1	4	4	5	5·52	1	2	1	1
Polygonum aviculare Linn.	2	1·02	..	2	..	..	..	..	..	..	..	..
P. convolvulus Linn.	2	0·20	2	..	..	..	2	0·20	2	..	..	..
Potentilla reptans Linn.	11	30·75	..	2	..	9	11	2·86	2	9	..	..
Prunella vulgaris Linn.	10	6·13	1	3	4	2	9	2·44	3	6	..	..

Hypochoeris radicata Linn.	2	0·20	2	..	..	..	1	0·20	1	..	..	..
Jasione montana Linn.	1	0·61	..	1	..	..	..	..	..	..	..	..
Juncus articulatus Linn.	2	0·20	2	..	..	..	7	0·82	6	1	..	..
J. bufonius Linn.	..	..	..	..	..	..	2	0·82	1	1	..	..
J. communis Mey.	5	0·41	5	..	..	..	9	4·08	5	3	1	..
Leontodon hispidum Linn.	2	0·41	2	..	..	..	2	0·20	2	..	..	..
Linaria elatine Mill.	2	0·41	2	..	..	..	..	..	..	..	..	..
L. spuria Mill.	4	1·43	3	1	..	..	2	0·41	2	..	..	..
Linum catharticum Linn.	7	2·04	4	3	..	..	4	1·02	2	2	..	..
Luzula campestris D.C.	1	0·20	1	..	..	..	5	0·41	5	..	..	..
Myosotis arvensis Hill.	2	0·20	2	..	..	..	1	0·20	1	..	..	..
Onopordon acanthium Linn.	4	0·82	3	1	..	..	..	..	..	..	..	..
Pedicularis sylvatica Linn.	1	0·20	1	..	..	..	..	..	..	..	..	..
Plantago lanceolata Linn.	7	1·63	3	4	..	..	2	0·61	1	1	..	..
P. major Linn.	6	1·63	3	3	..	..	5	1·22	4	1	..	..
P. media Linn.	10	29·27	1	1	4	4	5	5·52	1	2	1	1
Polygonum aviculare Linn.	2	1·02	..	2	..	..	..	..	..	..	..	..
P. convolvulus Linn.	2	0·20	2	..	..	..	2	0·20	2	..	..	..
Potentilla reptans Linn.	11	30·75	..	2	..	9	11	2·86	2	9	..	..
Prunella vulgaris Linn.	10	6·13	1	3	4	2	9	2·44	3	6	..	..
Ranunculus hederaceus Linn.	1	0·41	1	..	..	..	..	..	..	..	..	..
R. repens Linn.	11	19·35	..	6	1	4	12	17·50	..	5	4	3
Rubus fruticosus Linn.	2	1·02	1	1	..	..	4	0·82	2	2	..	..
Rumex acetosa Linn.	1	0·41	1	..	..	..	..	..	..	..	..	..
R. acetosella Linn.	4	0·41	4	..	..	..	..	..	..	..	..	..
R. obtusifolius Linn.	1	0·41	1	..	..	..	2	0·20	2	..	..	..
Senecio jacobaea Linn.	4	3·26	1	2	1	..	..	..	..	..	..	..
S. vulgaris Linn.	3	0·20	3	..	..	..	..	..	..	..	..	..
Sherardia arvensis Linn.	1	0·20	1	..	..	..	1	0·20	1	..	..	..
Sisymbrium officinale Scop.	..	..	..	..	..	..	1	0·20	1	..	..	..
Sonchus oleraceus Linn.	1	4·28	3	4	2	..	3	1·43	1	2	..	..
Spergula arvensis Linn.	..	..	..	..	..	..	1	0·20	1	..	..	..
Stachys arvensis Linn.	3	0·41	3	..	..	..	..	..	..	..	..	..
S. palustris Linn.	1	0·61	..	1	..	..	1	0·41	1	..	..	..
Taraxacum officinale Weber.	5	1·02	2	3	..	..	3	1·43	1	2	..	..
Urtica dioica Linn.	..	..	..	..	..	..	3	0·82	1	2	..	..
Veronica agrestis Linn.	1	0·82	..	1	..	..	..	..	..	..	..	..
V. officinalis Linn.	5	0·61	3	2	..	..	..	..	..	..	..	..
V. serpyllifolia Linn.	6	5·52	1	3	1	1	1	0·20	1	..	..	..
Viola arvensis Murr.	..	..	..	..	..	..	3	4·48	2	..	1	..
V. canina Linn.	6	2·65	2	4	..	..	..	..	..	..	..	..
Grasses:												
Alopecurus pratensis Linn.	1	0·20	1	..	..	..	5	0·82	4	1	..	..
Anthoxanthum odoratum Linn.	1	0·20	1	..	..	..	4	0·61	2	2	..	..
Agropyron repens Beauv.	1	0·20	1	..	..	..	..	..	..	..	..	..
Agrostis species	11	43·50	..	..	..	11*	12	36·95	..	2	2	8*
Arrhenatherum avenaceum Beauv.	1	0·20	1	..	..	..	2	0·20	2	..	..	..
Avena flavescens Linn.	..	..	..	..	..	..	2	0·20	2	..	..	..
Briza media Linn.	..	..	..	..	..	..	3	0·41	3	..	..	..
Cynosurus cristatus Linn.	3	0·20	3	..	..	..	7	2·44	2	5	..	..
Dactylis glomerata Linn.	2	0·20	2	..	..	..	5	0·82	3	2	..	..
Festuca pratensis Hackel.	1	0·20	1	..	..	..	3	0·20	3	..	..	..
F. rubra Linn.	10	4·70	3	6	1	..	11	4·08	4	6	1	..
Glyceria fluitans B.R.	1	0·20	1	..	..	..	2	0·20	2	..	..	..
Holcus lanatus Linn.	6	2·44	3	3	..	..	9	2·44	3	6	..	..
Lolium perenne Linn.	4	0·41	4	..	..	..	8	0·61	7	1	..	..
Phleum pratense Linn.	5	0·82	4	1	..	..	7	0·41	7	..	..	..
Poa annua Linn.	7	0·41	7	..	..	..	8	1·63	2	6	..	..
P. pratensis Linn.	2	0·61	1	1	..	..	..	..	..	..	..	..
P. trivialis Linn.	10	12·43	..	4	4	2	12	26·50	..	1	2	9†
Legumes:												
Lathyrus pratensis Linn.	1	1·22	..	1	..	..	1	0·20	1	..	..	..
Lotus corniculatus Linn.	3	1·02	1	2	..	..	4	1·63	3	1	..	..
L. tenuis Waldst and Kit.	2	0·20	2	..	..	..	1	0·20	1	..	..	..
Medicago lupulina Linn.	5	13·23	1	3	..	1	9	1·22	7	2	..	..
Trifolium campestre Schreb.	3	1·22	1	2	..	..	..	..	..	..	..	..
T. minus Sm.	4	0·82	2	2	..	..	4	1·43	2	2	..	..
T. pratense Linn.	4	0·41	4	..	..	..	3	0·41	3	..	..	..
T. repens Linn.	11	11·20	2	4	4	1	12	3·26	1	9	2	..
Vicia lathyroides Linn.	1	1·63	..	1	..	..	..	..	..	..	..	..

* *Agrostis* species: Drayton, 4 between 7·5 and 12·5 millions; 2 between 12·6 and 17·5; 2 between 17·6 and 22·5 and 3 over 22·5 million;
Dodwell, 5 ,, 0·5 ,, 6·0 ,, ; 2 ,, 6·1 ,, 11·5; 2 ,, 11·6 ,, 17·0 ,, 3 ,, 17·0 ,,

† *Poa trivialis:* Dodwell, 4 ,, 2·5 ,, 6·0 ,, ; 5 ,, 6·1 ,, 9·5; 2 ,, 9·6 ,, 13·0 ,, 1 ,, 13·5 ,,

TABLE 2. *Number of Viable Seeds (in Millions per Acre to a Depth of 7 in.) of each Species in a Third Year Ley, Arable, Ploughed Pasture, Corn Stubbles, and a 'Weed Sward' in Drayton and Dodwell*

	Drayton Third Year Ley		*Drayton Arable*			*Dodwell Arable*		*Dodwell Ploughed Pasture*		*Drayton Corn Stubbles*			*Drayton 'Weed Swards'*
Field Number	*1a*	*1b*	*12a*	*12b*	*17*	*28*	*31*	*23*	*24*	*9*	*13*	*15*	*2*
Miscellaneous species:													
Achillea ptarmica Linn.	..	..	..	0·20	..	..	..	..	..	..	..	..	..
Aethusa cynapium Linn.	3·06	6·32	1·02	1·22	0·61	1·84	1·43	7·95	..	1·02	0·82	0·20	0·20
Alchemilla arvensis Scop.	0·82	0·20	..	..	..	..	..	..	..	..	..	..	0·41
Allium vineale Linn.	..	0·20	0·41	1·22	0·41	0·20	..	..	..	0·41	2·65	0·41	0·20
Anagallis arvensis Linn.	4·28	3·06	3·67	2·65	10·20	3·46	3·06	6·13	2·44	4·90	4·08	10·60	8·78
A. caerulea Sm.	0·41	0·82	..	..	..	..	..	..	..	..	..	0·20	0·20
A. tenella Linn.	5·71	1·22	..	..	..	..	..	..	..	0·41	0·82	0·41	4·70
Bartsia odontites Huds.	..	1·22	..	1·22	..	0·20	1·02	0·20	..	2·86	..	0·61	1·02
Bellis perennis Linn.	1·02	..	2·86	2·86	..	..	..	..	..	3·46	1·02	8·58	1·63
Brassica campestris Linn.	..	..	..	..	..	..	..	..	..	..	0·20	..	..
B. sinapis Vis.	45·50	35·00	1·22	..	1·43	1·02	2·04	..	0·61	8·58	6·13	1·43	1·22
Cardamine hirsuta, Linn.	0·61	..	0·20	..	..	..	..	..	..	..	..	..	0·20
Carduus arvensis Robs.	..	0·41	0·61	0·20	..	..	..	..	..	..	0·41	..	0·82
C. palustris Linn.	..	..	0·20	..	..	..	..	0·20	..	..	..	..	0·20
Carex species	..	..	..	..	..	0·41	0·82	1·63	1·43	..	..	..	..
Cerastium vulgatum Linn.	0·61	0·20	..	1·43	1·22	0·41	..	0·20	..	0·61	0·61	..	0·82
Chenopodium album Linn.	..	..	..	..	..	1·02	..	..	..	..	..	0·20	0·20
Chrysanthemum leucanthemum Linn.	..	..	0·20	..	..	0·61	..	..	2·24	..	..	..	0·41
C. segetum Linn.	0·20	..	..	..	..	..	..	..	..	..	..	..	..
Daucus carota Linn.	..	..	..	..	..	..	..	..	..	..	0·20	..	..
Epilobium montanum Linn.	..	..	..	..	..	0·20	..	..	..	..	..	..	..
Euphorbia exigua Linn.	2·44	2·44	5·52	1·22	1·43	1·63	0·61	1·02	1·02	1·22	2·86	1·22	8·78
Galium mollugo Linn.	..	..	..	..	..	..	..	..	..	..	0·82	..	0·41
G. palustre Linn.	0·20	..	..	..	..	..	..	..	..	..	..	..	..
Geranium molle Linn.	0·41	..	0·20	0·20	..	..	..	..	..	..	..	..	0·41
Hypericum humifusum Linn.	0·20	..	..	..	..	..	..	0·41	0·41	..	..	..	..
H. perforatum Linn.	..	..	..	..	..	..	..	..	..	..	..	3·26	..
Juncus articulatus Linn.	..	..	..	..	..	0·20	..	..	..	..	..	..	..
J. bufonius Linn.	..	..	..	..	..	..	..	..	0·20	..	..	..	..
J. communis Mey	..	..	..	0·41	..	0·20	..	..	..	..	0·20	..	0·20
Linaria elatine Mill.	0·20	0·20	..	..	..	0·82	..	..	0·41	..	..	1·02	0·20
L. minor Desf.	..	0·20	..	..	..	..	0·41	..	..	..	..	0·41	..
L. spuria Mill.	..	..	1·84	..	..	0·41	..	6·13	1·84	0·82	0·41	8·58	1·63
Linum catharticum Linn.	2·04	4·28	..	0·20	0·41	..	1·22	1·02	0·61	2·86	0·41	7·35	2·44
Montia fontana	..	..	..	..	..	..	..	..	..	0·20	..	..	..
Myosotis arvensis Hill.	..	..	0·82	..	..	..	..	..	..	0·20	..	0·20	..
Ononis arvensis Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·20
Plantago lanceolata Linn.	..	..	0·41	..	..	..	..	..	..	..	..	0·20	..
P. major Linn.	0·82	..	2·44	2·86	0·41	..	..	..	..	3·67	3·46	5·71	0·41
P. media Linn.	3·67	3·87	5·31	4·48	1·63	0·20	..	1·43	4·48	1 43	0·41	3·06	2·86
Polygonum aviculare Linn.	..	..	3·26	0·61	0·20	..	..	0·20	..	0·61	0·61	..	..
P. convolvulus Linn.	0·41	0·82	0·20	0·20	..	..	..	..	..	..	0·20	0·20	0·41
Potentilla reptans Linn.	1·22	0·41	1·02	1·02	1·63	1·84	0·41	4·90	1·43	1·84	0·61	7·35	0·82
Prunella vulgaris Linn.	..	..	3·26	3·67	0·20	..	..	0·82	1·02	1·63	..	3·26	1·02
Ranunculus flammula Linn.	..	..	0·20	..	..	..	..	..	..	..	..	..	..
R. repens Linn.	4·90	1·02	2·44	15·50	5·71	3·67	1·22	2·04	4·90	3·67	8·37	26·50	..
Rumex acetosa Linn.	..	..	..	..	0·20	..	..	..	..	..	..	..	..
R. acetosella Linn.	0·20	..	..	..	0·41	..	..	..	..	..	..	..	..
R. obtusifolius Linn.	..	..	0·41	..	..	0·20	0·82	..	..	0·20	..	..	..
Sagina procumbens Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·20
Senecio vulgaris Linn.	..	..	..	..	..	0·41	..	..	..	..	..	..	0·41
Sherardia arvensis Linn.	..	..	0·20	..	..	..	..	..	..	..	0·20	..	2·04
Sonchus oleraceus Linn.	0·20	0·20	0·20	0·20	1·02	0·20	..	..	..	..	0·20	0·82	0·41
Stachys arvensis Linn.	..	0·61	0·41	..	..	0·20	0·41	..	..	1·84	..	..	0·41
S. palustris Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·41
Stellaria media Vill.	0·41	..	..	..	..	..	..	..	..	0·41	..	..	0·61
Urtica dioica Linn.	..	..	..	..	..	0·20	..	..	0·20	..	..	..	..
Veronica agrestis Linn.	..	..	..	..	..	..	..	..	..	..	0·20	..	..
V. officinalis Linn.	..	..	0·20	..	..	..	..	..	..	..	..	1·84	..
V. serpyllifolia Linn.	0·61	0·82	0·61	0·20	1·02	0·41	..	0·20	..	0·20	..	0·61	..

Chenopodium album Linn.	..	..	..	..	..	1·02	..	..	..	..	..	0·20	0·20	
Chrysanthemum leucanthemum Linn.	..	..	0·20	..	..	0·61	..	..	2·24	..	..	..	0·41	
C. segetum Linn.	0·20	..	..	..	..	..	..	..	..	..	..	..	..	
Daucus carota Linn.	..	..	..	..	..	..	..	..	..	..	0·20	..	..	
Epilobium montanum Linn.	..	..	..	..	..	0·20	..	..	..	..	..	..	..	
Euphorbia exigua Linn.	2·44	2·44	5·52	1·22	1·43	1·63	0·61	1·02	1·02	1·22	2·86	1·22	8·78	
Galium mollugo Linn.	..	..	..	..	..	..	..	..	..	..	0·82	..	0·41	
G. palustre Linn.	0·20	..	..	..	..	..	..	..	..	..	..	..	..	
Geranium molle Linn.	0·41	..	0·20	0·20	..	..	..	..	..	..	..	..	0·41	
Hypericum humifusum Linn.	0·20	..	..	..	..	..	..	0·41	0·41	..	..	..	..	
H. perforatum Linn.	..	..	..	..	..	..	..	..	..	..	..	3·26	..	
Juncus articulatus Linn.	..	..	..	..	..	0·20	..	..	..	..	..	..	..	
J. bufonius Linn.	..	..	..	..	..	..	..	..	0·20	..	..	..	..	
J. communis Mey	..	..	..	0·41	..	0·20	..	..	..	..	0·20	..	0·20	
Linaria elatine Mill.	0·20	0·20	..	..	..	0·82	..	..	0·41	..	..	1·02	0·20	
L. minor Desf.	..	0·20	..	..	..	..	0·41	..	..	..	..	0·41	..	
L. spuria Mill.	..	..	1·84	..	..	0·41	..	6·13	1·84	0·82	0·41	8·58	1·63	
Linum catharticum Linn.	2·04	4·28	..	0·20	0·41	..	1·22	1·02	0·61	2·86	0·41	7·35	2·44	
Montia fontana	..	..	..	..	..	..	..	..	..	0·20	..	..	..	
Myosotis arvensis Hill.	..	..	0·82	..	..	..	..	..	..	0·20	..	0·20	..	
Ononis arvensis Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·20	
Plantago lanceolata Linn.	..	..	0·41	..	..	..	..	..	..	..	..	0·20	..	
P. major Linn.	0·82	..	2·44	2·86	0·41	..	..	..	..	3·67	3·46	5·71	0·41	
P. media Linn.	3·67	3·87	5·31	4·48	1·63	0·20	..	1·43	4·48	1 43	0·41	3·06	2·86	
Polygonum aviculare Linn.	..	..	3·26	0·61	0·20	..	..	0·20	..	0·61	0·61	..	..	
P. convolvulus Linn.	0·41	0·82	0·20	0·20	..	..	..	..	..	..	0·20	0·20	0·41	
Potentilla reptans Linn.	1·22	0·41	1·02	1·02	1·63	1·84	0·41	4·90	1·43	1·84	0·61	7·35	0·82	
Prunella vulgaris Linn.	..	..	3·26	3·67	0·20	..	..	0·82	1·02	1·63	..	3·26	1·02	
Ranunculus flammula Linn.	..	..	0·20	..	..	..	..	..	..	..	..	..	..	
R. repens Linn.	4·90	1·02	2·44	15·50	5·71	3·67	1·22	2·04	4·90	3·67	8·37	26·50	..	
Rumex acetosa Linn.	..	..	..	..	0·20	..	..	..	..	..	..	..	..	
R. acetosella Linn.	0·20	..	..	..	0·41	..	..	..	..	..	..	..	..	
R. obtusifolius Linn.	..	..	0·41	..	..	0·20	0·82	..	..	0·20	..	..	..	
Sagina procumbens Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·20	
Senecio vulgaris Linn.	..	..	..	..	..	0·41	..	..	..	..	..	..	0·41	
Sherardia arvensis Linn.	..	..	0·20	..	..	..	..	..	..	..	0·20	..	2·04	
Sonchus oleraceus Linn.	0·20	0·20	0·20	0·20	1·02	0·20	..	..	..	..	0·20	0·82	0·41	
Stachys arvensis Linn.	..	0·61	0·41	..	..	0·20	0·41	..	..	1·84	..	..	0·41	
S. palustris Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·41	
Stellaria media Vill.	0·41	..	..	..	..	..	..	..	..	0·41	..	..	0·61	
Urtica dioica Linn.	..	..	..	..	..	0·20	..	..	0·20	..	..	..	..	
Veronica agrestis Linn.	..	..	..	..	..	..	..	..	..	..	0·20	..	..	
V. officinalis Linn.	..	..	0·20	..	..	..	..	..	..	..	..	1·84	..	
V. serpyllifolia Linn.	0·61	0·82	0·61	0·20	1·02	0·41	..	0·20	..	0·20	..	0·61	..	
Viola arvensis Murr.	0·41	..	0·20	..	..	..	0·20	..	..	..	..	..	..	
V. canina Linn.	..	..	..	..	..	..	..	..	..	..	0·61	..	..	
Grasses:														
Agropyron repens Beauv.	..	..	..	..	..	..	..	..	..	..	..	0·20	..	
Agrostis species	4·90	2·04	0·20	0·82	0·82	2·04	2·04	6·52	8·37	3·06	0·41	10·60	5·31	
Alopecurus pratensis Linn.	..	..	..	..	..	..	..	..	..	..	..	0·41	..	
Arrhenatherum avenaceum Beauv.	..	..	..	..	..	..	0·20	..	..	..	..	..	1·22	
Avena flavescens Linn.	..	..	..	..	..	..	..	..	..	..	..	..	0·20	
A. sativa Linn.	..	..	..	..	..	..	0·20	..	..	..	..	..	..	
Brachypodium pinnatum Beauv.	..	..	..	..	..	..	..	..	..	0·20	..	..	..	
Bromus arvensis Linn.	..	..	..	0·20	..	..	..	..	..	..	..	..	..	
Dactylis glomerata Linn.	..	0·41	..	..	..	0·61	..	..	..	..	0·20	0·20	..	
Deschampsia caespitosa Beauv.	..	..	..	..	..	..	..	..	..	0·20	..	..	..	
Festuca pratensis Hackel	..	0·20	..	..	..	..	..	..	..	..	..	..	..	
F. rubra Linn.	..	..	..	..	0·20	..	..	..	1·84	..	0·20	0·20	0·20	
Holcus lanatus Linn.	..	..	..	..	..	..	..	0·20	..	..	..	..	..	
Lolium italicum Braun.	..	0·82	..	..	..	..	..	..	..	..	..	..	..	
L. perenne Linn.	..	1·02	..	..	..	..	..	..	..	..	..	..	..	
Phleum pratense Linn.	..	0·20	..	..	0·41	..	..	..	..	0·20	..	..	..	
Poa annua Linn.	..	..	..	..	..	..	0·20	..	..	..	0·61	..	..	
P. trivialis Linn.	0·20	0·20	..	1·84	0·41	0·41	0·41	0·41	..	0·20	1·02	0·20	1·43	
Legumes:														
Lotus tenuis Waldst. and Kit.	..	0·20	..	..	..	..	..	..	..	..	..	..	..	
Medicago lupulina Linn.	14·05	12·43	0·82	..	..	..	0·41	..	..	0·61	3·46	..	1·02	
Trifolium campestre Schreb.	0·61	1·43	0·20	..	..	..	0·20	..	..	..	1·43	..	0·41	
T. minus Sm.	3·26	28·35	0·20	..	..	..	..	..	..	..	0·41	..	..	
T. pratense Linn.	0·20	0·20	..	..	..	..	..	..	..	..	..	..	..	
T. repens Linn.	..	..	..	..	0·20	..	..	0·20	0·20	..	..	2·24	0·20	

Results

The numbers of seedlings of each species obtained from the soils of the Drayton permanent pasture fields are given in Table 1. Certain species are outstanding in having occurred in most or all of the eleven fields, and in this group the largest maximum quantities of seedlings per acre have been given by *Ranunculus repens* (creeping buttercup), *Potentilla reptans* (cinquefoil), *Plantago media* (hoary plantain), *Agrostis* spp. (bent grasses), *Poa trivialis* (rough-stalked meadow grass), and *Trifolium repens* (wild white clover). *Medicago lupulina* (trefoil) occurred in only five of the fields, but its maximum quantity exceeded that for *Trifolium repens*. The frequency groups in Table 1 clearly indicate that the majority of the species had more small quantities than larger quantities of buried viable seed among their soil populations. Among the 88 species of this table are numerous typical arable weeds, which indicates that most of these fields were in arable cultivation before they 'tumbled down' to poor permanent grass. There are some valuable agricultural grasses among the 17 species observed, but the populations of the majority are small when compared with those for *Agrostis*. No fewer than 9 species of legumes have appeared, including those from only one field, and of these 6 have given over one million seedlings to the acre.

Field No. 10 of this category could best be described at the time of sampling as 'scrub with pasture', and the soil was extremely water-logged. The maximum quantities for *Hypericum humifusum* (trailing St. John's wort), *Carex* species (sedges), and *Holcus lanatus* (Yorkshire fog) (Table 1) were all derived from this particular field. Seedlings of *Ulex europaeus* (gorse) and *Rubus fruticosus* (bramble) were also found in this soil; but even in such a seemingly derelict milieu there were also present seedlings of the better grasses and of *Trifolium repens*. The presence of seedlings of certain arable species indicates a previous state of cultivation.

The results from the 12 permanent pasture fields of Dodwell also show the predominance of certain species, and in some instances the same species were also the most frequent in Drayton. The largest maximum quantities were given by *Ranunculus repens*, *Agrostis* spp., and *Poa trivialis*, as judged by the Drayton standard of abundance, but differences between these permanent pasture fields of the two farms are shown by the number of species being fewer in Dodwell (75 as compared with 88 in Drayton), and the much smaller populations of the seedlings of each species. Compared with the other species in Table 1, therefore, *Cerastium vulgatum* (mouse-ear chickweed), *Hypericum humifusum*, *Bellis perennis*, *Anagallis arvensis* (scarlet pimpernel), and *Plantago media* have given large quantities of seedlings in addition to the three species previously mentioned. There was a somewhat larger proportion of grasses and legumes to miscellaneous plants from the soils of these fields compared with Drayton. The quantities for *Cynosurus cristatus* (crested dog's tail) are worthy of note, for previous experiments have given very small densities of buried viable seed of

this grass, and of *Lolium perenne* (perennial ryegrass). Each of the 16 grass species occurring in the Dodwell pastures appeared in the soils of more than one field. Again, the frequencies throughout show a decided preponderance of small quantities over large quantities of seedlings for the majority of the species. Typical arable weeds are also present, but not to the marked extent as at Drayton. Species characteristic of badly drained pastures, however, are much more common. The conclusion is, therefore, that these Dodwell pastures were older swards and of probably better origin in regard to seeding-down than the corresponding Drayton permanent pastures. An instance of the abundance of a grass in the surface-vegetation but the absence of its seedlings with regard to buried viable seed occurred in field 25, described as an 'old Tor pasture'. The soil from this field gave rise to the seedlings of 30 species of plants, among which was the largest maximum quantity for *Holcus lanatus* and nearly 22 million seed per acre of *Agrostis* spp.; but not a single seedling of *Brachypodium pinnatum* (Tor grass) arose from this field or from the other 11 permanent pastures at Dodwell.

The results from the third-year ley at Drayton are given in Table 2. This field was sampled in two parts, 1*a* and 1*b*, as the surface-vegetation showed that there had been a difference in treatment. The data indicate that the whole field had been under arable conditions for some years. Numbers of the same species occurred in both parts and their density in several instances is reasonably close, but a difference in history is seen in that, of the species which occur in only one part of the field, many more miscellaneous species have arisen from the soil of 1*a*, and there were 5 more grass species, all of the cultivated type, from 1*b*. Arable species from the buried viable-seed flora of this field are, in general, numerous, whilst the very large populations of *Brassica sinapis* (charlock), trefoil, and *Trifolium minus* (yellow suckling clover) are noteworthy.

There were two arable fields at Drayton (Nos. 12 and 17), the buried viable-seed flora of which is given in Table 2. Owing to an obvious difference in pre-treatment field 12 was sampled in two parts, 12*a* and 12*b*. Most of the species which occurred in these soils were also present in the soils of the pasture fields, but in these particular fields the species associated with arable land are dominant. Especially is this the case in the relation of their densities to those of the grasses and clovers, the small populations for *Agrostis* spp. and *Poa trivialis* being especially noticeable. A difference in pre-treatment in the two parts of field 12 is observable, more particularly in regard to those species which occurred in either the one or the other part. Seedlings of *Allium vineale* (crow garlic or wild onion) arose from the soils of fields 12 and 17, the population from 12*b* being of appreciable size. An instance of a dissimilarity between the surface-vegetation and the viable-seed flora of the soil beneath occurred in field 12, where plants of *Carduus arvensis* (creeping thistle) constituted so thick a crop that it was difficult to walk among the mass of prickly herbage, but as the data indicate, only small quantities of the seedlings of this species arose from the soils of this field.

At Dodwell there were two arable fields (Nos. 28 and 31), and also

two ploughed permanent pasture fields (23 and 24), of which particulars are given in Table 2. A similarity in the viable-seed data is observable between these Dodwell arable fields and those of Drayton in that certain species gave comparatively large populations of seedlings in each case, and also the same species occur in numerous instances. Some differences are, however, apparent, e.g. the absence of any seedlings of *Polygonum aviculare* (knotgrass) and *P. convolvulus* (black bindweed), and also the extremely low population of *Plantago media* in the Dodwell arable.

The buried viable-seed flora from the ploughed pasture fields is somewhat similar to that for the permanent pastures, for they were sampled not long after they had been ploughed. Certain species are outstanding in their comparatively great density, the most striking being *Agrostis* spp., *Potentilla reptans*, *Aethusa cynapium* (fool's parsley), *Linaria spuria* (fluellen), and *Anagallis arvensis* in one or both fields. The presence of the seedlings of *Festuca rubra* (red fescue) in field 24, and of *Trifolium repens* in both fields, is noticeable.

Table 2 also shows the species, with the numbers of seedlings, which occurred in the soils from three corn stubbles at Drayton. Among the large number of species are those which have appeared from pasture and arable fields, and certain of these have given populations of great density. Seedlings of *Allium vineale* have occurred in appreciable quantity from field 13, whilst field 9 has provided the only instance of seedlings of *Brachypodium pinnatum*, which was referred to in connexion with field 25 in the pasture group of Dodwell. The large populations of *Plantago major* (broad-leaved plantain) from each field and the comparatively large number of grass species present in these corn-stubble soils is interesting. The greater density of many species in field 15, compared with the same species for the other two fields, presumably denotes a difference in previous cropping history.

The buried viable-seed data for 'the weed sward' at Drayton (Table 2) show an unexpected absence of *Ranunculus repens* among the 43 species forming the flora from its soil. The populations for *Anagallis arvensis*, *A. tenella* (bog pimpernel), *Euphorbia exigua* (dwarf spurge) and *Agrostis* spp. are outstandingly large, whilst those of several other species have given between 1 and 2 million seedlings per acre. The results indicate that this field, the surface of which had neither the partly bare soil of arable nor was dominated by even the poorest grasses, had been in all probability under arable cultivation for many years, as is shown by the nature and number of seedlings which arose from its soil.

The data from the soils of the 5 extra fields at Drayton are given in Table 3. They are all characterized by having very dense populations of *Ranunculus repens* and, to a lesser extent, of *Poa trivialis* and *Trifolium repens*. The numbers for *Agrostis* spp. are surprisingly low. It must be remembered that these data relate only to a period of 14 months, and this much shorter time of investigation would have influenced the results in a comparison with the two years for the soils in general. The species are of a grassland type, but some are also found in arable land. The grasses and legumes are well represented although the density of some species is very small. Field 46 had a more numerous flora

than the remainder, which indicates a somewhat different pre-treatment.

TABLE 3. *Number of Viable Seeds of each Species in Millions per Acre to a Depth of 7 in. Drayton Extra Fields, chiefly Permanent Pasture Nos. 42–6*

Species	Field No. 42	43	44	45	46
Miscellaneous species:					
Agrimonia eupatoria Linn.	..	..	..	..	0·20
Anthemis cotula Linn.	..	..	..	..	0·41
Bellis perennis Linn.	0·20	0·20	..	0·41	0·82
Carduus arvensis Robs.	..	..	0·82	..	1·02
Carex species	..	0·20	0·41	0·20	..
Cerastium vulgatum Linn.	0·82	1·84	3·26	4·48	1·22
Chenopodium album Linn.	0·41	..	..	..	..
Chrysanthemum leucanthemum Linn.	0·20	..	0·41	..	1·43
Galium palustre Linn.	..	..	..	..	0·20
G. verum Linn.	..	..	..	..	0·41
Geranium dissectum Linn.	..	..	..	0·20	..
Hypochoeris radicata Linn.	..	..	..	..	0·20
Juncus bufonius Linn.	0·20	..	..	..	..
J. communis Mey.	0·20	..	0·61	0·41	..
Linaria minor Desf.	..	0·41	..	..	..
Onopordon acanthium Linn.	..	..	0·41	..	..
Potentilla reptans Linn.	0·20	1·02	0·41	2·04	..
Prunella vulgaris Linn.	..	..	..	..	0·20
Ranunculus repens Linn.	6·32	26·10	8·37	4·90	6·13
Rumex acetosella Linn.	..	..	..	..	0·41
R. crispus Linn.	..	0·20	..	..	..
Senecio jacobaea Linn.	..	..	..	..	0·20
Sonchus oleraceus Linn.	..	..	..	0·61	0·20
Taraxacum officinale Weber	0·41	..	..	0·20	0·41
Urtica dioica Linn.	0·41	..	..	..	0·61
Veronica agrestis Linn.	..	..	..	..	0·20
V. serpyllifolia Linn.	0·61	..	..	..	0·20
Grasses:					
Agrostis species	0·41	0·41	0·82	0·41	0·20
Cynosurus cristatus Linn.	..	0·20	0·20	..	..
Dactylis glomerata Linn.	..	0·20	..	0·20	..
Festuca rubra Linn.	..	..	..	0·20	..
Holcus lanatus Linn.	0·41	..	0·20	..	0·20
Lolium perenne Linn.	..	..	..	0·41	..
Phleum pratense Linn.	..	..	..	..	0·20
Poa annua Linn.	0·20	0·20	..	..	..
P. pratensis Linn.	..	..	..	..	0·20
P. trivialis Linn.	2·44	4·28	7·15	6·32	11·80
Legumes:					
Lathyrus pratensis Linn.	..	..	..	0·41	..
Medicago lupulina Linn.	..	..	..	0·61	1·22
Trifolium minus Sm.	..	0·41	..	..	0·20
T. pratense Linn.	..	..	..	..	0·41
T. repens Linn.	1·22	6·93	0·82	1·22	3·87
Vicia lathyroides Linn.	..	..	0·20	1·43	1·02

As previously mentioned, the soils were put out in May 1940 and seedlings began to appear in June. The dates at which identification became possible and counts made were noted over the two-year period, and the information thus obtained has shown that a large number of species germinated immediately and appeared during the summer and autumn of the same year. During 1941 other species appeared, whilst a very few species did not germinate until the spring of 1942.

The chief germinating periods and also the periods at which germinations took place to a lesser degree for certain species are given in Table 4, in which the species have been arranged according to the commencement of the appearance of their seedlings. The unusual period of November to April in which *Allium vineale* germinated, the extremely brief period for *Bartsia odontites* (red bartsia), and the dormancy of *Veronica agrestis* (procumbent speedwell) and of *Stachys arvensis* (field woundwort) until 1942, are in marked contrast to the majority of the species, whilst the data as a whole show that there was a considerable spreadover in the periodicity of germination among the numerous species occurring in these soils, and that certain of them exhibited delayed germination. This factor in the germination of buried seeds was also observed in the previous work on pastures [4], when dormancy of the seeds of the same species but from different habitats was consistently exhibited. In this earlier experiment, however, the soils were under observation for 3 years.

Discussion

One of the chief disclosures of the data has been the repeated occurrence, often in considerable amounts, of the same species in the soils of all the classes of fields investigated. In general, however, the evidence points to the greater densities of viable-seed populations of species that are usually associated with arable conditions in the soils of fields which have in fact been arable or under a temporary ley. That numerous arable species should have been found in the soils of the permanent pastures is not surprising, for most of these particular fields were probably under arable-crop production in the years around 1918. The fact that the soils beneath these pastures contained the seeds of numerous arable species, even though they may have been sown down to grass again 20 years before the samples for this experiment were taken in 1940, is to be expected, for similar earlier work on pastures [4], in which the ages of the sward were known, showed that the soils beneath swards of over 50 years' duration still contained viable seeds of typical arable species.

It is of interest that the buried-seed flora has indicated that individual fields and, in some instances, parts of the same field, have obviously had different cultural treatment from others of the same class. This has happened in those fields which have been under crop-rotation, whilst among the permanent-pasture group there has been evidence of the longer sward-duration of the fields at Dodwell, and the presence of certain species characteristic of badly drained pasture has indicated that excess of water has prevailed in many of the grass fields.

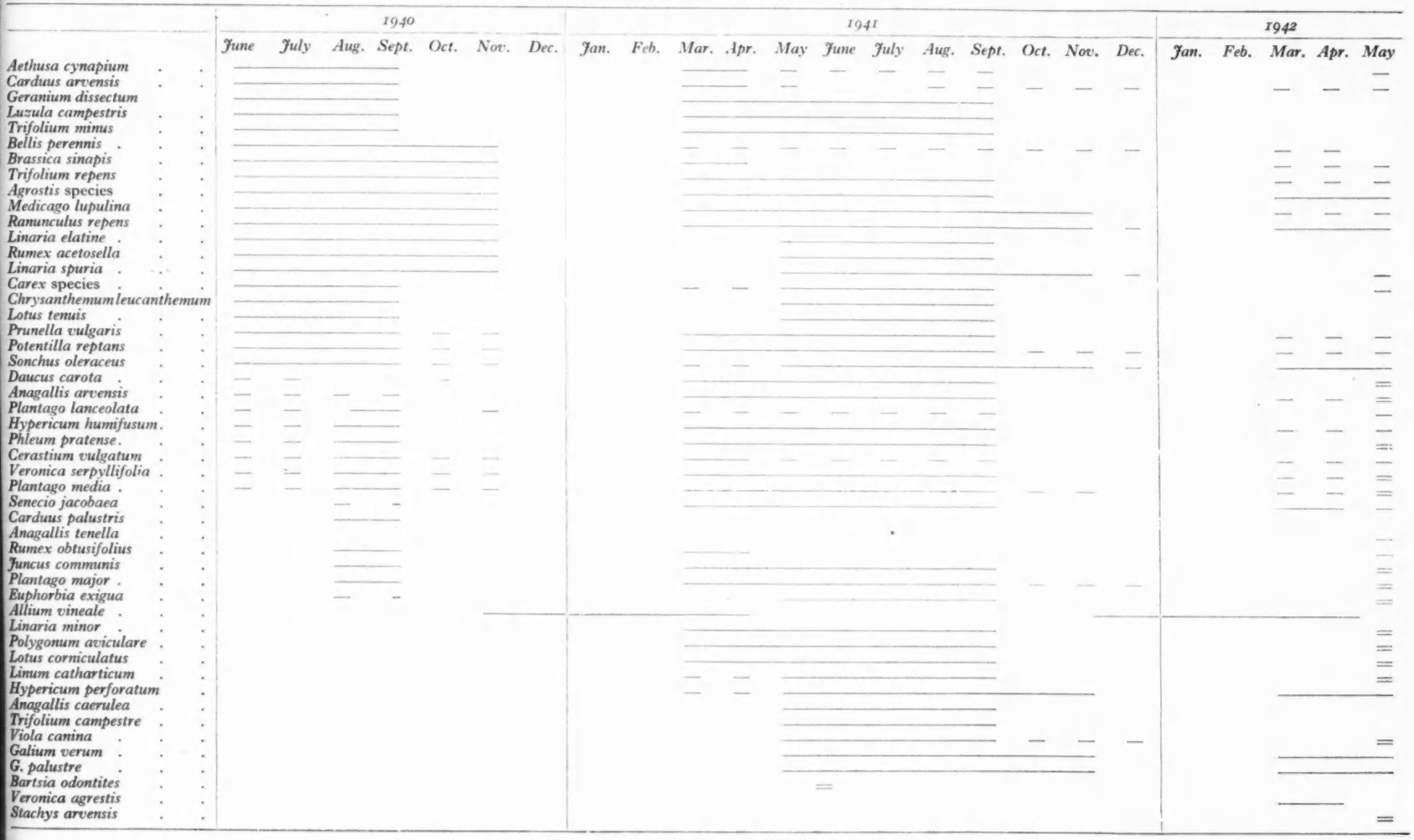
The distinct periodicity of germination which has been observed among the species over the two years of investigation has shown that they fall into groups. The observations on the seasonal periodicity of germination in the earlier work on pastures [4], compared with the results of Brenchley and Warington [2, 3], have demonstrated that plants characteristic of pasture differ from those of arable soils in this respect. In a later work Brenchley [8] states that comparatively few species germinate freely throughout the year, most species showing definite periodicity. It is interesting that all germinations of *Bartsia odontites* (red bartsia) from the soils at Drayton and Dodwell took place in June of the 1941 period. This month is at the end of the periodicity of germination time given by Brenchley for this species, as the seedlings appear during the first half of the year.

Agriculturally, one of the chief findings of the survey as a whole is the presence in these calcareous soils of the seeds of numerous valuable leguminous species. In some fields the density of *Medicago lupulina*, *Trifolium repens*, and *Lotus corniculatus* is very appreciable, and that of the other six species is quite significant. The occurrence of these legumes in kind and quantity is in marked contrast to the corresponding viable-seed data from the non-calcareous soils of the two earlier investigations [4, 5]. Among the grasses, however, the same low populations for the majority of the cultivated species in relation to those for the miscellaneous herbs has been observed. It was this disparity of the surface-vegetation of grassland and the viable seed of grass species in the soil beneath, which led to the deduction that most of the grass species depend upon vegetative reproduction in maintaining their position in swards. Further evidence of this was provided from the investigation of swards at different elevations, and of a salt marsh [9]. It is significant, however, that even in an instance of extreme neglect, as was mentioned in connexion with field 10 at Drayton, some viable seeds of the better grasses and of *Trifolium repens* were present in the soil.

The quantities of the buried viable seed of the miscellaneous species from these soils are comparable in numbers to those which occurred in the Cahn Hill Improvement Scheme survey [5]. In the discussion of those data an example in which the numbers of viable seeds in the soil of a field and of a hill area were expressed in pounds of seed per acre (by the use of the known weight-per-thousand-seed of the species) and compared with the weight of seeds used in typical seeds-mixtures, showed that the weight of the seeds buried in the field soil exceeded that of the heavier mixture by over three times. It may be mentioned that the weight of seeds in the hill soil did not equal the weight of seeds in the simpler mixture consisting of fewer species and less seed-weight per acre. That great quantities of viable seeds exist in soils is not surprising in the light of the data given by Salisbury [10], which reveal the enormous seed output and average reproductive capacity of a single plant of the numerous species investigated.

The survey-method of soil sampling with a borer does not provide data as to the buried viable-seed content of successive layers of soil of known depth, as in the pasture investigation [4], but in the present

TABLE 4. *The Chief Germinating Periods (marked with a Continuous Line) and the Minor Germinating Periods (marked with a Dash) of Certain Species during the Months of the Experiment*



Note: = signifies a chief germinating period (June 1941 and May 1942)

instance two permanent-pasture fields were sampled from 7 to 14 in. below the surface by taking a second boring at the base of the first boring. Thirteen species in all occurred in these bore-hole samples, 4 in one and the remainder in the other field soil. Of these species 4 were grasses, of which *Agrostis* spp. gave the largest number of seedlings, whilst of the miscellaneous species *Juncus communis* was the most numerous. The densities of all the species were low compared with those at the higher level. Few buried viable seeds occurred below the plough-level, thus confirming the observation of the earlier trial [4] in which the greatest concentrations of seed occurred from 1 to 7 in. below the surface, and much lower concentrations down to 12 in. in the lowland soils. In this investigation there were indications that greater concentrations of viable seed occurred in wet soils, and the Cahn Hill survey, and the later work previously referred to [9], confirmed this finding. The waterlogged condition of many of the Drayton fields, and to a lesser extent of those at Dodwell, owing to the choked watercourses, would therefore of itself favour dense concentrations of buried viable seed. As Brenchley and Adam [11] pointed out in discussing data on the recolonization of 2 areas of land of a widely differing moisture-content, an excess of water is not an isolated factor, for associated with it are deficient aeration and a lowering of soil temperature. It is possible, therefore, that these conditions, particularly that of insufficient aeration, may have a preservative effect on the vitality of seeds in the soil.

The comparatively small number of seedlings of *Deschampsia caespitosa* and more especially of *Brachypodium pinnatum* in the pasture soils shows that most of the seeds shed by these plants do not succeed in entering the soil. Two analogous instances occurred in the Cahn Hill survey [5]: few buried seeds of *Nardus stricta* Linn. and *Molinia caerulea* Moench occurred even in those soils where these grasses were dominant in the herbage. Jefferies [12] has stated that the small seeds of *Molinia* germinate in the cracks on exposed soil and in the tangle of dead leaves in hollows, giving rise to a great number of seedlings. It is possible that similar surface-germination may take place with *Deschampsia caespitosa*, but with the much larger-seeded *Brachypodium pinnatum* the probability is that other natural causes prevent the seed entering the soil. The extent to which these two grasses set seed in these Midland soils is a matter of surmise. *Deschampsia caespitosa*, being of a tufted habit of growth, probably relies almost exclusively on seed-production for its spread to fresh ground, but *Brachypodium pinnatum* has a well-developed vegetative means in addition. Hornby [13] mentions the creeping habit of this species, and in describing its abundance in certain boulder-clay areas in Northamptonshire suggests that the deficiency of phosphates in these particular soils may assist the spread of Brachypodium, because the useful grasses and clovers are discouraged by the lack of this plant-food. Hutchinson [14] also illustrates how this species spreads by underground stems with clusters of buds, and mentions that the plant colonizes by means of its seed, which ripens in late summer. Measures to prevent flowering are enumerated among the methods for

control in down pastures. With regard to seed-setting in *Deschampsia caespitosa*, Beddows [15] reports that a single uncovered plant growing in a greenhouse during 1941 produced viable seed. These seeds would seem to be the result of self-fertilization, as there were no other plants of this species in the vicinity. It is probable, therefore, that under natural conditions where cross-fertilization is also possible the seed will be readily set. It may be pointed out that Lewis [16] mentions having found several distinct strains of this grass, and describes the differences in vegetation and time of flowering of a tall and of a leafy dwarf-type. *Carduus arvensis* is in another category because the viable-seed populations of it in the soils have been vastly out of proportion to its abundance in the herbage, particularly of field 12. Salisbury [10] mentions that the reproduction by seed of this species is often slight or non-existent, owing to all the flowers on any individual plant being either functionally male or female, though structurally hermaphrodite, and quotes Hayden [17], who states that fruit is set freely only when the plants of the two sexes are within 100 ft. of one another. On the other hand, according to Rodgers [18] [quoted in 10] the vegetative extension of *Carduus arvensis* can be as much as 20–40 ft. in a single season. The buried viable-seed populations of *Allium vineale* are important on account of the losses which this plant can cause in a wheat crop, and by tainting of dairy products. Although its density in the soils has not been great, its abundance in arable fields has been described [6]. Two varieties of this plant are mentioned by Salisbury [10], *v. capsuliferum*, having an inflorescence consisting of flowers only, and *Allium compactum*, which produces no flowers but a head of numerous bulbils; whilst Tinney [19], after describing the vegetative means of reproduction which this plant adopts in soft and hard ground bulbs and aerial bulbils, gives details of cultivation and cropping measures whereby this species can be completely eradicated from badly infested land. It is thus apparent that the amount of seed present in a viable condition in the soil has little, if any, relation to the quantity of *Allium vineale* which may occur in the surface-herbage.

The constant appearance of miscellaneous herbs or weeds in cultivated land constitutes, of course, one of the main problems in crop production. All investigations into the buried viable seed of soils have disclosed the fact that large quantities of seed are always present and only awaiting surface cultivation to cause them to germinate. This has proved to be the case particularly in lowland and semi-lowland soils. As was mentioned in discussing the data of the Cahn Hill Improvement Scheme [5], in the process of cultivation only a small proportion of the soil comprises that shallow layer at the surface in which seeds may germinate; thus a limit is imposed on the number of seedlings from buried seed which appear after a tillage operation. When cultivating to a depth of 7 in. the proportion of seeds that would germinate would vary from one species to another according to its minimum, optimum, and maximum depth for germination, and certain conditions of cultivation might increase the seedling populations of some miscellaneous species and diminish those of others. A bare fallow designed to reduce

weeds would have to be cultivated frequently and deeply throughout a season in order to bring as many viable seeds as possible to the correct germinating level. Brenchley [8] has pointed out that in the usual fallow the stirrings are not frequent enough to ensure reducing the viable weed-seed numbers in the soil, and describes the vigorous seed-setting capacity of weed species in land that is being fallowed. In connexion with the problem Stapledon [20] has advocated particular rotations and crops for use in the control of weeds on the intake fields of hill farms on which situations infestation is often severe. Davies [21] gives cultural methods on the re-seeding of the neglected Drayton and Dodwell type of pasture, and of the treatment when weeds infest a new ley, whilst Wilks [22] has described detailed methods of cultivations and the type of implement to be used in the preparation for the growing of corn and beans on this heavy land. The fact that certain species of agricultural value also have their buried viable-seed populations cannot be overlooked, and the degree of seed-density of such species as *Poa trivialis* and *Trifolium repens* is a decided advantage in assisting the formation of a new sward, and even in the procuring of a seed crop, whilst the numbers of seed of the remaining better grasses and legumes constitute in the aggregate a quantity that can be of value.

Acknowledgements

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Appendix

The common names of the following species are not given in the text:

Achillea millefolium Linn. Yarrow.
A. ptarmica Linn. Sneezewort.
Agrimonia eupatoria Linn. Agrimony.
Alchemilla arvensis Scop. Parsley piert.
Anthemis cotula Mey. Mayweed.
Brassica campestris Linn. Field cabbage.
Capsella bursa-pastoris Medik. Shepherd's purse.
Cardamine amara Linn. Large bittercress.
C. hirsuta Linn. Hairy bittercress.
Carduus palustris Linn. Marsh thistle.
Centaurea nigra Linn. Knapweed.
Chenopodium album Linn. Fat hen.
C. glaucum Linn. Glaucous goosefoot.
Chrysanthemum leucanthemum Linn. Ox-eye daisy.
C. segetum Linn. Corn marigold.
Conopodium denudatum Koch. Earthnut.
Crepis paludosa Moench. Marsh hawk's-beard.
Daucus carota Linn. Wild carrot.
Epilobium montanum Linn. Broad-leaved willow herb.
E. palustre Linn. Marsh willow herb.
Galium mollugo Linn. Hedge bedstraw.
G. palustre Linn. Marsh bedstraw.
G. verum Linn. Lady's bedstraw.
Geranium dissectum Linn. Cut-leaved cranesbill.
G. molle Linn. Dove's foot cranesbill.
Hieracium pilosella Linn. Mouse-ear hawkweed.
Hydrocotyle vulgaris Linn. Marsh pennywort.
Hypericum perforatum Linn. Common St. John's wort.
Hypochoeris radicata Linn. Cat's ear.
Jasione montana Linn. Sheep's bit.
Juncus articulatus Linn. Jointed rush.
J. bufonius Linn. Toad rush.
J. communis Mey. Common rush.
Leontodon hispidum Linn. Common hawkbit.
Linaria elatine Mill. Pointed-leaved toadflax.
L. minor Desf. Lesser toad-flax.
Linum catharticum Linn. Cathartic flax.
Luzula campestris D.C. Field woodrush.
Montia fontana Linn. Blinks.
Myosotis arvensis Hill. Field forget-me-not.
Ononis arvensis Linn. Rest-harrow.
Onopordon acanthium Linn. Scotch thistle.
Pedicularis sylvatica Linn. Lousewort.
Plantago lanceolata Linn. Ribgrass.
Prunella vulgaris Linn. Selfheal.
Ranunculus flammula Linn. Lesser spearwort.
R. hederaceus Linn. Ivy-leaved crowfoot.
Rumex acetosa Linn. Sorrel dock.
R. acetosella Linn. Sheep's sorrel.
R. obtusifolius Linn. Broad-leaved dock.
R. crispus Linn. Curled dock.
Sagina procumbens Linn. Procumbent pearlwort.
Senecio jacobaea Linn. Ragwort.
S. vulgaris Linn. Groundsel.
Sherardia arvensis Linn. Field madder.
Sisymbrium officinale Scop. Hedge mustard.
Sonchus oleraceus Linn. Sow thistle.
Spergula arvensis Linn. Corn spurrey.
Stachys palustris Linn. Marsh woundwort.
Stellaria media Vill. Chickweed.
Taraxacum officinale Weber. Dandelion.
Urtica dioica Linn. Common nettle.
Veronica officinalis Linn. Common speedwell.
V. serpyllifolia Linn. Thyme-leaved speedwell.
Viola arvensis Murr. Field pansy.
V. canina Linn. Dog violet.

Agropyron repens Beauv. Couch grass.
Alopecurus pratensis Linn. Meadow foxtail.
Anthoxanthum odoratum Linn. Sweet vernal grass.
Avena flavescens Linn. Golden oat grass.
A. sativa Linn. Cultivated oat.
Briza media Linn. Quaking grass.
Bromus arvensis Linn. Field brome.
Dactylis glomerata Linn. Cocksfoot.
Festuca pratensis Hackel. Meadow fescue.
Glyceria fluitans Br. Floating meadow grass.
Lolium italicum Braun. Italian ryegrass.
Phleum pratense Linn. Timothy grass.
Poa annua Linn. Annual meadow grass.
P. pratensis Linn. Smooth-stalked meadow grass.
Lathyrus pratensis Linn. Meadow vetchling.
Lotus corniculatus Linn. Bird's-foot trefoil.
Trifolium campestre Schreb. Hop trefoil.
T. pratense Linn. Red clover.
Vicia lathyroides Linn. Spring vetch.

THE VALUE OF PASTURE FOR MEAL-FED PIGS

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Introduction.—It is a common practice in New Zealand to supplement the pig's ration, mostly skim milk or whey, with a good pasture (rye-grass and white clover) run [1], and in the Argentine pigs, fed largely on maize, are run on old lucerne paddocks [2]. So far as we are aware, however, no experimental work in these two areas has been done to determine to what extent the grazing effected a saving of other feeding-stuffs.

At the instigation of the Agricultural Research Council an investigation was commenced at the beginning of May 1942 to determine the value of pasture as a supplement to pigs being fed a meal ration.

In England interest in this question has been aroused by the recent investigations of Crowther [3, 4] who, in the course of trials extending over three seasons, found that by feeding pigs a very much restricted ration of meal supplemented with young mown grass of high quality (e.g. lawn clippings) a satisfactory rate of live-weight increase was obtained and an average saving of 35 per cent. in the use of meal effected, as compared with pigs fed an all-meal ration. In one case, with a fixed allowance of 1½ lb. of meal, a saving of the order of 65 per cent. was secured without measurably increasing the length of the fattening-period.

The importance of these findings, in relation to war-time pig production, needs no emphasis, and it was felt that the question was worthy of further investigation. In the present work, however, a different method of approach to the problem has been adopted. Since the outlay in labour and equipment involved in continually mowing and hand-feeding grass greatly restricts, if not completely prohibits, the adoption of this procedure in commercial practice, it was considered most desirable to discover whether the spectacular saving in meal consumption achieved in Crowther's experiments could be duplicated under conditions where the fattening pigs had to forage grass for themselves. Information was required relating to the period from shortly after weaning until the time the pigs reached bacon-weight.

Attention must first be directed to a recent paper by Woodman and Evans [5], published since our work was commenced. They made a comprehensive survey of the literature relating to the value of grass in pig nutrition and reported upon a large-scale carefully conducted feeding trial which has not confirmed Crowther's findings. It is difficult to explain the contradictory results obtained, for in the two investigations the general method of approach to the problem was the same. In each case the meal consumption of groups of pigs fed lawn-clippings as a supplement to a severely restricted daily ration of meal was compared with that of a control group on an all-meal ration.

The Experiment

Briefly, the plan of the experiment has been as follows: A line of suitable pigs from the Cambridge inbred strain of Large Whites was divided into two groups, balanced for live-weight, sex, and litter. One group, the 'controls', was housed indoors and fed a standard qualitative ration (Table 1) according to a pre-determined live-weight rationing

TABLE 1. *Composition of Meal Ration*

	Parts by weight	
Constituent	*Up to 140 lb. live-weight*	*From 140 to 200 lb. live-weight*
Middlings . .	30	15
Barley meal . .	60	80
White fish meal .	10	5
Lucerne meal .	2	2

scale (Table 2). The second group, termed the 'grass' group, was also housed indoors under comparable conditions, but the pigs of this group were allowed access to a pasture run-off throughout the experimental period. This group received the same qualitative ration as the control group, but in amounts so regulated that the pigs made the same rate of

TABLE 2. *Live-weight Rationing Scales*

Live-weight (lb.)	*Pounds meal per pig per day*		*Live-weight (lb.)*	*Pounds meal per pig per day*	
	Trial I	*Trial II*		*Trial I*	*Trial II*
30	..	2·00	120	5·75	5·75
40	..	2·50	130	6·00	6·00
50	2·50	3·00	140	6·25	6·25
60	3·00	3·50	150	6·50	6·50
70	3·50	4·00	160	6·75	6·75
80	4·00	4·50	170	6·95	6·95
90	4·50	4·85	180	7·05	7·05
100	5·00	5·10	190	7·10	7·10
110	5·50	5·50	200	7·20	7·20

growth as that of the controls. This regulation was effected by weighing each group of pigs once weekly and increasing or reducing the ration fed to the 'grass' group according as their rate of live-weight increase tended to lag behind or outstrip that of the control group.

In using the live-weight rationing scale given in Table 2 to adjust the ration of the control group each week, the procedure adopted was to read off the allowance for each pig on the basis of its particular live-weight and sum these individual allowances: not by the alternative method of calculating the allowance from the average live-weight of the group.

In order to ensure that the ration fed remained qualitatively standard for the duration of the experimental period, supplies of the ingredients

of the ration were purchased in bulk at the commencement of the investigation. With regard to the composition of the ration employed, it should be noted that this contained approximately 2 per cent. of lucerne meal, to supply vitamins to the control animals. Unless this precaution were taken, the possibility existed that any difference noted favouring the performance of the 'grass' group might be due to the ration of the controls being deficient in respect to vitamin-content.

A careful week-to-week record was kept of the nutritive condition of the pasture in the run-off provided.

The first 'grass' and control groups, each consisting of 6 pigs, were started on the treatments on May 3, 1942, after being accustomed to the experimental ration for a ten-day period. The trial continued for 14 weeks, concluding on August 7, 1942, by which time the most forward pig had reached 200 lb. live-weight. Later more pigs became available and the experiment was repeated with control and 'grass' groups each comprised of 10 pigs. This second trial ran for just over 20 weeks—from July 17, 1942, until December 3, 1942.

The first trial proceeded without disturbance, but in the 17th week of the second trial a gilt of the control group contracted erysipelas. This animal was immediately discarded (November 10, 1942) and all animals in both groups were injected to prevent a possible spread of the infection. This injection caused no apparent check in the growth of the animals, these cleaning up their food in a normal manner.

In order that the two groups might remain strictly comparable a gilt was also removed from the 'grass' group. By good fortune it proved possible, on recourse to the growth-curves of the individual animals, to select for discard an animal of precisely similar weight and possessing an almost identical growth-curve.

Results

The data resulting from the two trials are summarized in Tables 3 and 4.

Reference to column (1) of these tables, in which the average live-weight of 'grass' and control groups is listed for successive weeks, shows that reasonable success was achieved in regulating the growth-rate of the 'grass' pigs to conform with that of the controls.

As previously pointed out, the first trial was conducted during the late spring and summer months, and the second was held during the late summer and autumn months. The nutritive state of the pasture varied greatly between the two periods and also at different times within each trial. For this reason it is essential that the results of the two trials be considered separately. Nor can the rate of growth of the two sets of control animals be compared, since for the second trial the live-weight rationing scale was raised. It was considered that the relatively more efficient gains made by the 'grass' animals in the early stages of the first trial might not have been obtained had the level of feeding of the controls been higher. It was reasoned that a higher plane of nutrition for the controls should lead to a more rapid rate of growth, and this in turn result in a shortened fattening-period, reduced maintenance costs, and

TABLE 3. *Data from Trial I*

Date	(1) Average live-wt. (lb.)		(2) Meal consumption per pig per day (lb.)		(3) Meal saved per day by each 'grass' pig	(4) Consumption of 'grass' pigs as % of consumption of controls	(5) Cumulative meal consumption per pig		(6) Cumulative saving per 'grass' pig	(7) Nutritive state of pasture
	Control	Grass	Control	Grass			Control	Grass		
3/5/42	53·6	53·9					..	..	..	Feed scarce but of high quality
8/5/42	59·3	60·6	2·70	2·70	0·00	100·0	13·5	13·5	0·0	Rapid growth
15/5/42	66·0	66·9	2·97	2·83	0·14	95·3	34·3	33·3	1·0	,, ,,
22/5/42	72·4	74·9	3·30	3·17	0·13	96·1	57·4	55·5	1·9	Abundant growth of good quality
29/5/42	80·2	81·6	3·67	3·17	0·50	86·4	83·0	77·7	5·3	,, ,, ,,
5/6/42	86·7	88·6	4·00	3·50	0·50	87·5	111·3	102·2	9·1	,, ,, ,,
12/6/42	94·7	95·3	4·33	3·67	0·66	84·8	141·4	127·8	13·6	,, ,, ,,
19/6/42	104·3	103·0	4·75	4·08	0·67	85·9	174·6	156·4	18·2	Quality starting to deteriorate
26/6/42	111·5	110·2	5·00	4·50	0·50	90·0	209·6	187·9	21·7	Becoming rather stemmy
3/7/42	122·4	118·2	5·33	5·00	0·33	93·8	247·0	222·9	24·1	Very stemmy. No young growth
10/7/42	129·7	127·1	5·67	5·00	0·00	100·0	286·6	262·6	24·0	Very dry. No young growth
17/7/42	140·8	137·5	5·92	6·17	−0·25	104·2	328·0	305·7	22·3	,, ,, ,,
24/7/42	147·4	147·5	6·00	6·66	−0·66	111·0	370·0	352·4	17·6	Slight improvement—but only
31/7/42	156·3	155·5	6·33	6·33	0·00	100·0	414·3	396·7	17·6	very limited amount of grazing
7/8/42	170·1	167·8	6·33	7·00	−0·67	110·6	458·7	445·7	13·0	available

TABLE 4. *Data from Trial II*

Date	(1) Average live-wt. (lb.) Control	(1) Average live-wt. (lb.) Grass	(2) Meal consumption per pig per day (lb.) Control	(2) Meal consumption per pig per day (lb.) Grass	(3) Meal saved per day by each 'grass' pig	(4) Consumption of 'grass' pigs as % of consumption of controls	(5) Cumulative meal consumption per pig Control	(5) Cumulative meal consumption per pig Grass	(6) Cumulative saving per 'grass' pig	(7) Nutritive state of pasture
17/7/42	33·1	33·1					..	..	..	Not abundant but of good quality
24/7/42	35·8	36·0	1·65	1·65	0·00	100·0	11·6	11·6	0·0	Good growth
31/7/42	38·1	39·3	1·80	1·80	0·00	100·0	24·2	24·2	0·0	Good—both in amount and quality
7/8/42	39·8	40·8	2·00	1·90	0·10	95·0	38·2	37·4	0·8	" " " " "
14/8/42	43·8	45·6	2·50	2·20	0·30	88·0	55·7	52·9	2·8	" " " " "
21/8/42	48·0	49·6	2·70	2·30	0·40	85·2	74·6	69·0	5·6	" " " " "
28/8/42	55·1	58·1	2·90	2·50	0·40	86·2	94·9	86·4	8·5	" " " " "
4/9/42	63·1	63·7	3·25	2·85	0·40	87·7	117·6	106·4	11·2	" " " " "
11/9/42	69·4	70·0	3·65	3·25	0·40	89·0	143·2	129·2	14·0	Deteriorating due to dry weather
18/9/42	77·3	77·1	3·90	3·50	0·40	89·7	170·5	153·7	16·8	
25/9/42	80·9	80·5	4·30	3·90	0·40	90·7	200·6	181·0	19·6	Little grass—very dry
2/10/42	90·0	87·9	4·40	4·10	0·30	93·2	231·4	209·7	21·7	
9/10/42	99·2	98·4	4·70	4·70	0·00	100·0	264·3	242·6	21·7	Grass coming away
16/10/42	106·8	105·5	5·10	5·10	0·00	100·0	300·0	278·3	21·7	
23/10/42	114·9	114·9	5·35	5·60	−0·25	104·7	337·4	317·5	19·9	Abundant grass—very wet
30/10/42	123·0	121·4	5·55	5·70	−0·15	102·7	376·3	357·4	18·9	Ground boggy
6/11/42	*132·7 †134·0	*131·4 †133·1	5·80	6·20	−0·40	106·9	416·9	400·8	16·1	Adequate grazing but soiled due to wet conditions
13/11/42	143·3	143·5	5·95	6·83	−0·88	114·8	458·5	448·6	9·9	" " " " "
20/11/42	149·3	151·1	6·33	7·22	−0·89	114·1	502·8	499·1	3·7	" " " " "
27/11/42	160·4	159·5	6·44	7·33	−0·89	113·8	547·9	550·5	−2·6	" " " " "
3/12/42	165·3	165·5	6·22	7·11	−0·89	114·3	585·2	593·1	−7·9	Grass very poor and ground much pugged

* Average of ten pigs. † Average excluding pig discarded on 10/11/42.

more efficient live-weight gains. With the 'grass' pigs fed at a higher level it was thought probable that their desire to supplement the meal ration by foraging pasture would be considerably reduced, so that they might derive small if any benefit from being allowed access to it.

Considering Trial I (Table 3), it may be noted from col. (7) that at the beginning of the experimental period grass was not very abundant, but that what was available was in a young and nutritive stage of growth. During the following few weeks the pasture rapidly improved both in amount and quality, but thereafter, due to the onset of dry weather, slowly deteriorated, becoming very stemmy with little or no young growth. During the last few weeks of the trial the condition of the pasture was just starting to improve somewhat as a result of rain. There was, however, still very little grazing available at the time the trial concluded.

In col. (2) the meal consumption per pig per day of the control and 'grass' groups is given for successive weeks. From col. (3) it may be seen that the difference in consumption between the two groups on a pig-per-day basis gradually increased over the first 6 weeks of the trial and reached the maximum figure of 0·67 lb. At this stage the meal consumption of the 'grass' pigs was approximately 85 per cent. of that of the controls. This corresponded with the period when abundant good-quality herbage was available. As the grazing became poorer this difference in favour of the 'grass' pigs was gradually reduced and then eliminated altogether. Finally, during the dry period when no young grass was available, the grass pigs came to need more meal than the controls, receiving 0·67 lb. more meal per pig per day. Figures given in cols. (5) and (6) show that, at the end of the period favouring the 'grass' pigs (i.e. July 3, 1942) these had each consumed 24 lb. less meal than had the controls. This difference was, however, largely eliminated in the later stages of the trial when drought conditions prevailed.

The results from Trial II closely resemble those just outlined for Trial I. Again, the grass was at first not very abundant, but improved rapidly and remained reasonably good in both quantity and quality until a little more than half-way through the trial (i.e. about September 25, 1942). It was then deteriorating due to dry weather conditions. This dry spell was not very prolonged and during the last 6 or 7 weeks of the trial abundant grass was available. During this final period, however, the weather became very cold, the ground very wet and pugged, and the pasture in the later stages soiled and unattractive.

From cols. (2) and (7) of Table 4 it may be seen that the improvement which took place in the pasture during the first few weeks of the trial was associated with a decline in the meal consumption of the grass pigs relative to that of the controls. By the 5th week of the trial the 'grass' group required 0·4 lb. less meal per pig per day. The difference was maintained at this level until the end of the 10th week of the trial, by which time the pasture had become poor. By the end of the 12th week both groups were again consuming equal amounts and by the beginning of the 17th week the 'grass' pigs required approximately 0·9 lb. more meal per day than the controls in order to make the same rate of growth. This higher consumption of the 'grass' pigs continued until the trial

was concluded at the end of the 20th week. As previously mentioned, conditions were by this time very cold and wet.

The data shown in cols. (5) and (6) in respect to the cumulative meal consumption per day at successive periods indicate that had the 'grass' group been shut away from their run-off at the end of the 11th week, a saving in meal consumption of approximately 22 lb. per pig might have been made. Allowing the pigs to remain on the run-off during the subsequent period, when pasture-growth and weather conditions were unfavourable, resulted in the 'grass' pigs each consuming over the whole trial, not 22 lb. less meal but approximately 8 lb. more meal than did the controls.

Summary and Conclusions

(*a*) A method has been described for determining the value to fattening pigs of a pasture run-off as a supplement to a generous meal ration. In modified form this method might well be used with various species of farm stock to determine the value of many varieties of succulent crops under range conditions, and to study the effects of other environmental factors such as occur in practice.

(*b*) Results have been obtained which suggest that by allowing pigs of between 30 and 120 lb. live-weight access to pasture in a young and nutritive stage of growth, a saving in meal consumption of the magnitude of 0·4 to 0·7 lb. meal per pig per day may be expected.

(*c*) Evidence has been advanced which indicates that live-weight gains are less efficient in respect to meal consumption, if pigs are allowed access either to a grass run-off of poor nutritive value, as is usually the case under drought conditions, or to a reasonably good run-off under cold and wet conditions.

(*d*) From the data resulting from the two trials described, it is not possible to decide whether any benefit in respect to efficiency of live-weight gains is to be derived from allowing pigs of 120–200 lb. access to a first-class pasture run-off.

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THE FEEDING OF ACORNS TO LAYING PULLETS AND DUCKS

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Introduction.—Discoloration of egg-yolks due to laying birds having access to acorns has long been recognized. As early as 1904 a general caveat appeared in a German periodical [1] to the effect that when acorns are fed in too large quantities to hens they cause a more or less black coloration of egg-yolk. Later, in 1915, an abstract appeared in the *Journal of the Board of Agriculture* [2] of an observational trial carried out in Germany and reported in the *Deutsche Tierärztliche Wochenschrift*. The addition of 1 oz. per head daily of decorticated, dried, and powdered acorns to the normal rations for laying birds resulted in a diminution and finally a cessation of egg-production. The vitelline membrane and yolk-contents of the eggs which were laid were of a dirty brown colour, which was attributed to the oxidation of the acorn tannin. The adverse effects on production were ascribed partly to the astringent action of tannin on the ovarian yolk-secreting capillaries and to lowered absorption of digested protein from the intestines. Three days after withholding acorns, egg-production was resumed and gradually increased.

A recent publication by Olsen [3] confirms that acorns can cause yolk discoloration. Thirty per cent. of a flock of birds having access to acorns of the white oak (*Quercus alba*) laid eggs with olive-coloured yolks. In subsequent tests hens housed in battery-cages and fed rations containing 25 and 50 per cent. of ground white-oak acorns produced, after 4 days' feeding, eggs which had olive-coloured yolks. A similar result was obtained when the diet contained 25 per cent. of the ground acorn husks or 25 per cent. of whole acorns from the black oak (*Quercus velutina*).

On the other hand, Cranfield [4] fed, without detriment to egg-production or yolk-colour, dried ground acorns to 17 laying birds at the rate of 2 oz. per head daily, an amount which represented almost 50 per cent. of their total food. Bakker [5] has recently reported a similar result. He used up to 40 per cent. of minced fresh acorns in the daily rations for 7 laying birds. During a feeding period of 4 months the egg-yield fluctuated between 50 per cent. and 70 per cent. of possible production. Yolk-colour was normal until towards the end of the test, when a slight greenish tinge occurred that was not sufficiently pronounced to be noticed by unsuspecting consumers.

Similar contradictory results of acorn-feeding have been expressed in the columns of the weekly poultry press, but lack of precise information of the quantities and kind of acorns fed has limited the interpretation.

At the National Institute of Poultry Husbandry we have received during the spring and autumn months each year samples of off-coloured new-laid eggs produced by both hens and ducks having access to grass

runs. Usually the water-supply and the rations which have been fed cannot be held responsible. As a routine method of investigation, trap-nesting the flock (where this is possible), and isolating the birds which are responsible, is a prelude to dividing them into two groups and allowing one-half access to the run and permanently housing the remainder. Invariably the trouble disappears in the birds which are confined to the house, and so reduces the cause to the run. A botanical survey has in some instances revealed the presence of acorns together with weeds, such as shepherd's purse (*Capsella bursa-pastoris*), which is widely distributed in established poultry-runs, and to a lesser extent penny cress (*Thlaspi arvense*). Both of these weeds have been described by Payne [6] as causing olive-coloured yolks when they are eaten by laying stock, a conclusion which was unsupported by more recent work by Albright and Thompson [7]. Such discordant experimental results, and the absence of information concerning the effects of other flora present, have made impossible the positive identification of the plants responsible in particular instances.

The severity of the poultry-food rationing system coupled with a fierce competition for short supplies of coupon-free foodstuffs has compelled the farmer either to effect a drastic reduction in stock or alternatively to implement his resources by using home-grown materials not required for humans. The poultry press, adopting the principle that no potential food-source however small in quantity relative to needs should be despised, has repeatedly drawn the attention of its readers to the nutritive possibilities of natural food materials. The wide distribution of the oak in the British Isles and the encouraging chemical composition of the dry matter of the acorn, which is similar in many respects to that of barley, have proved stimulatives to organized schemes for the collection and sale of acorns for stock-feeding.

The position is not now simply a question of isolated poultry flocks having the opportunity of picking up small quantities of acorns with possible harmful effects, but of the intentional inclusion of acorns as part of the normal diet. Consequently, in designing the present experiment it seemed desirable in addition to observations on egg-quality to obtain timely information on the quantitative effects on health and egg-production resulting from the substitution of part of the ration by varying proportions of acorns.

Unfortunately, the quantity of acorns at our disposal did not allow for the feeding of groups large enough to permit of statistical evaluation. Advertisements soliciting additional supplies met with no response, and the entire quantity made available was due to the industry of local school children. This circumstance had a compensating feature, as the species of oaks from which the acorns were collected were identified. The two varieties of the English oak (*Quercus robur*) provided the entire collection, the bulk being from the commoner variety, *pedunculata*, in which the individual acorns are supported from the branch by long footstalks. In the variety *sessiliflora*, occasional trees of which grow in the district, the acorns are borne in clusters directly seated upon the branch, and some of this variety were included in the experimental material.

The Experiment

The stock used for the experiment consisted of 16 pullets and 8 ducks, which were housed in individual laying cages in separate battery houses. Both types of stock were divided into four groups of equal size. The birds in Group 1 acted as a control and were provided with a daily ration of a balanced laying mash at the rate of 5 and 6 oz. per head for pullets and ducks, respectively. The remaining groups received the same rations as Group 1 save that acorns were included, commencing with 1 oz. per bird daily and increasing the quantities at 10-day intervals to 2 and finally 3 oz., equivalent weights of mash being withheld. The quantities of acorns thus progressively constituted 20, 40, and 60 per cent. of the daily food-intake for the hens, and 16·6, 33·3, and 50 per cent. of the food provided to the ducks.

For Group 2 the acorns were germinated before feeding until the sprouts were from $\frac{1}{8}$ to $\frac{1}{4}$ in. long. The ripe ungerminated acorns fed to Group 3 were boiled for one hour, the cooking water being discarded. Group 4 were provided with ripe ungerminated acorns. All three types of acorns were crushed before being mixed with the remainder of the ration and fed to both hens and ducks in the form of a wet mash. In all cases both husk and kernel of the acorns were fed. All eggs produced were candled prior to internal examination.

Observations.—The interior quality of all eggs laid by the ducks and hens in Group 4, receiving rations containing ripe ungerminated acorns, was normal even when the quantity of acorns fed was increased to 3 oz. per head daily. At this maximum level the food did not appear to be unpalatable and no difficulty was experienced in persuading the birds to eat any of the three forms in which the acorns were fed. The droppings compared with those of the controls (Group 1) appeared to be normal when the daily intake of all three forms in which the acorns were fed to the hens did not exceed 1 oz. per head. When this was increased to 2 oz. the excreta from the hens in Groups 2, 3, and 4 became darker in colour and reduced in quantity. Raising the intake to 3 oz. of acorns produced a markedly costive effect, and egg-production eventually ceased to be resumed when the quantity was again reduced to 2 oz. per day. The egg-production and droppings of the ducks did not appear to be affected in any of the three acorn-fed groups, even at the maximum level of acorns. Three days after increasing the quantities of germinated and boiled acorns to 2 oz. daily, yolk-discoloration appeared in the eggs from both hens and ducks, being more pronounced in the case of the birds receiving the cooked acorns. This off-coloration was observed in the eggs from only one hen and one duck having germinated acorns and from two hens and one duck eating boiled acorns, the remaining birds which stayed in production continuing to lay normal eggs when the levels of both types of acorns were finally increased to 3 oz. At this maximum quantity of acorns the egg-yolks from the individual birds which were responsible became decidedly objectionable in colour, more especially in the groups receiving cooked acorns. The yolk-colour of the new-laid eggs, described by reference to Ridgway's Colour Standard [8], varied from chamois

and colonial buff (a perceptible greenish-brown tinge) in the eggs from the birds consuming germinated acorns, to olive-buff, olive-lake, and dull citrine (dark greenish-brown shades), where cooked acorns were being fed. Eggs from the control group were in the colour-range between wax yellow and pale and light orange yellow.

Successive eggs from individual birds tended to remain a constant shade of yolk-colour. When these eggs were examined before a candling lamp the yolks appeared very dark and the whites a light shade of green. In no case, however, did the white show any discoloration when the internal egg-contents were subsequently examined, and the apparent greenish tinge observed at candling must be due to reflection of light from the discolored yolk, an effect which has been described by Pennington [9]. When the egg-contents were allowed to stand at a room temperature of 50–60° F. for 24 hours, the yolks became still darker in colour. Increased discoloration did not appear to result when the whole eggs were stored at 50° F. for periods up to 10 days and then opened for examination of their contents. The olive pigmentation was not confined to the vitelline membrane but extended throughout the entire yolk.

When affected eggs were soft boiled for 3½–4 minutes the yolk-contents resembled black treacle in appearance, and independent co-operators not conversant with the cause of the condition observed that they had a bitter flavour and tasted strongly of ink. On hard-boiling the eggs and cutting cross-sections of the contents, the discoloration was confined to a central core in the yolk, the remainder of the yolk and the white being perfectly normal. This effect was more readily seen when the yolk was poached, the white having previously been removed to prevent veiling of the yolk and so facilitate the observation of colour changes. The yolk-colour became progressively darker up to about three-minutes cooking, after which the yolk-surface gradually turned to a light shade of yellow. Inspection of sections of the yolks after they had cooled revealed the same appearance as had been observed in hard-boiled eggs. Identical observations were noted when the off-coloured eggs were fried.

Discussion

Having corroborated the findings of other workers in demonstrating that acorns may under certain conditions cause yolk-discoloration, it seemed desirable to examine the chemical processes involved in order to determine the reasons why, in the experiences of the present test, ripe ungerminated acorns failed to produce off-coloured yolks, and boiled acorns resulted in more pronounced discolorations than raw germinated acorns, although both forms were fed in equal amounts.

Acorns are known to be rich in tannins, which are recognized to exercise a physiologically costive effect, a fact that in the present experiment would account for the decrease in quantity of droppings produced by the hens with increasing intakes of all forms of acorns (ducks appear to be more resistant). The chemistry of the tannins is complex. They have been classified by Perkin and Everest into three groups according to their hydrolytic products: (*a*) gallotannins or depsides, which yield gallic acid; (*b*) ellagitannins, which give ellagic acid; and (*c*) phlobo or

catechol tannins, which are hydrolysed to phlobaphene. The oak is rich in gallotannin, which is the most important tannin belonging to the first of these groups. On hydrolysis gallotannin is converted into digallic acid and glucose, and on further breakdown the digallic acid yields gallic acid as a final end-product.

Samples of the boiled acorns used in the present test indicated that an appreciable hydrolysis of the tannin bodies had taken place. This was reflected in the large proportion of gallic acid present as such and found in the ether-extract of the material (gallotannin and digallic acid being only sparingly soluble in ether). The dark colour of the water-extract of the boiled acorns deepened slowly on boiling and rapidly became a very dark brown on the addition of caustic soda: an observation to be expected from an extract containing gallic-acid bodies, owing to the absorption of oxygen from the air. The raw ungerminated acorns contained only traces of gallic acid, which may occur naturally associated with gallotannin or from a partial hydrolysis occurring in storage. The water-extract of the raw acorns was much lighter in colour, darkening with caustic soda more slowly, presumably due to a slow formation of gallic acid as the tannin is hydrolysed by the caustic soda solution. The water-extract from the acorns which had germinated was almost as dark as that from the boiled acorns, the gallic acid present approaching that contained in the extract of boiled acorns.

Such analytical findings, considered in conjunction with the effects on yolk-colour which resulted, suggest that gallic rather than digallic acid is responsible, since the relative quantities of gallic acid present in the boiled and germinated acorns correspond to the intensity of yolk-discolorations which occurred, the yolk remaining normal in colour where the birds were receiving raw acorns containing only traces of gallic acid.

As a confirmatory test weak solutions of gallic and digallic acids were mixed with normal coloured yolks from eggs produced by the control birds, and the mixture raised to the normal body-temperature of the hen. Within 24 hours a slatey-olive discoloration, similar in appearance to that seen in the off-coloured eggs produced in the feeding trial, occurred in the gallic-acid and yolk mixtures. The digallic acid, however, caused a pinkish tinge which was not typical of any of the discolorations observed during the feeding of acorns.

The reactivity of gallic acid with ferric salts to yield black precipitates, which is made use of in the manufacture of ink, suggests a similar chemical effect in the present instance, since, as Lesné and co-workers [10] have shown, iron does not exist in egg-white, which was unaffected by the feeding of any of the three forms of acorns used, whereas the yolk contains an appreciable store, varying according to Erikson *et al.* [11] from 6·82 to 7·85 mg. of iron per 100 gm. of egg-yolk. Hill [12] considers the inorganic iron in egg-yolk to resemble colloidal ferric hydroxide in properties, and it would therefore be in a reactive form. This is supported by the frequently observed dark ring at the partition between the yolk and white of a hard-boiled egg that forms during the cooling of the egg when the iron of the yolk reduced to the ferrous state combines with sulphur derived from egg-white amino acids to form ferrous sulphide.

That the yolk-discoloration in the present instance is due to the formation of ferric gallate would seem to be further confirmed by the description of the inky flavour of the yolks. It was not found possible, owing to the relatively small quantities present, to isolate ferric gallate in the egg-yolks.

The duck which had been fed on cooked acorns and had consistently laid eggs with badly discolored yolks was killed at the conclusion of the test. The ovary contained many ova in various stages of development, one being practically mature and another partially shelled in the oviduct. The yolk of the latter was slightly discolored, the remaining ova appearing to be perfectly normal.

Several ova were removed from their follicles and placed in a biological incubator together with the contents of the egg which had been removed from the oviduct. At the end of 24 hours yolk-discoloration had intensified in the more mature egg, and was now present in the next ova to be shed, the remaining ova showing no discoloration. The bird appeared to be perfectly healthy and no degenerative tissue changes were discernible. It would seem from this that gallic acid is added as a constituent of egg-yolk, and that chemical interaction with yolk-iron, and consequently progressive discoloration, take place during the passage of the egg down the oviduct and after it is laid.

Summary

Although the scale of the experiment provided only observational groups, it would appear that it is safe to include ripe ungerminated acorns as part of the rations for laying hens and ducks. When such material constituted up to 20 per cent. of the daily food-intake of hens and ducks, no adverse effects on health and production resulted. Raising the quantity of ripe ungerminated acorns for hens to 40 and 60 per cent. of the daily ration produced a costive condition of the droppings, and at the higher level an immediate and substantial fall in egg-production, which may be due in part to the precipitation of food protein by tannic acid in the digestive tract, to be later voided in an insoluble form in the faeces. Increasing the quantity of ripe ungerminated acorns to 33·3 and 50 per cent. of the food given to the ducks did not appear to affect either egg-yield or the physical condition of the droppings, but the numbers of birds involved do not permit of general recommendations. The experiences of the present test afford an explanation of the apparently contradicatory results of acorn feeding.

Complaints of discolored yolks attributed to birds picking up acorns from the range are almost exclusively confined to the early spring and late autumn, when presumably suitable temperature encourages the germination of the acorns, a process which results in the conversion of appreciable amounts of gallotannin to gallic acid. This does not preclude the possibility of unripe acorns, blown from the trees by gales, being dangerous, since no opportunity of determining the gallic-acid constitution of such material was possible.

Yolk-discoloration is usually restricted to a small percentage of a flock having access to acorns, and this was confirmed in the experiment now

reported, since with the same quantitative intake of germinated and boiled acorns, the adverse condition was confined to individual ducks and hens.

In species of animals that are dependent for the perpetuation of future generations on the food-reserve of the egg, it is not surprising that the normal individual should be equipped with an adequate mechanism to prevent toxic food materials from being included.

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THE FATTENING OF PIGS ON SWILL ALONE: A MUNICIPAL ENTERPRISE

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Introduction.—The chemical composition and nutritive value of different types of swill have been discussed by Woodman [1] and by Woodman and Evans [2]. The purpose of the present communication is to describe a large-scale experiment in swill-feeding which has been carried out since August 1940 by the Metropolitan Borough of Paddington, and to discuss briefly the potentialities of this type of management as a permanent feature of British pig husbandry.

Paddington, except for its 27-acre recreation ground, is an entirely built-up residential district, with a substantial hotel area in the south-west; its total population in 1939 was 140,000, but this figure has been considerably reduced during the past two years. It now operates the largest municipal pig-fattening scheme in Great Britain, and in two years has produced over 700,000 lb. of pig-meat entirely from unsupplemented kitchen waste, with a net profit to the borough, after deduction of one-fifth annually of the total capital expenditure, of over £4,500.

The enterprise has been carried out from the beginning as an official borough activity, under the direct supervision of the Parks Superintendent (J. L.). This policy, which was adopted in preference to forming a 'pig club', has necessitated the foregoing of supplies of meal, but appears to have been amply justified by results. It is noteworthy that neither the Parks Superintendent nor any of his assistants had any previous experience of pig-keeping.

At the commencement few pigs only were fattened, and the numbers were built up gradually to the present levels. The method of dealing with the swill and the system of management have likewise been modified or elaborated as experience has been gained. Current procedures alone are described in this paper.

Much of the success which has attended the experiment must be attributed to propaganda, both national and municipal; the co-operation of the public has been sustained throughout, and the value of the scheme to the borough is generally appreciated. In considering the financial aspects of the scheme, which is conducted on a strictly commercial basis, it must be remembered that the kitchen waste now utilized so successfully would formerly have been removed by canal from Paddington, to be dumped on waste ground. This procedure was expensive, entailing a cost of 12*s.* to 15*s.* per ton of total refuse, whereas the edible swill is now sold to the piggeries at 30*s.* per ton. (This additional revenue to the Council is not included in the 'profit' figure cited above.)

Collection, composition, and treatment of swill.—Both private residences and hotels yield large quantities of kitchen waste, which in pre-war days would have been collected for dispatch by canal to be dumped on waste land.

The public has been encouraged to separate the suitable forms of waste, which is collected twice or thrice daily from both private and street bins and sorted carefully both at the collection centre and after transportation (by lorry) to the piggeries. The average collection is 200 tons per month.

The approximate average composition of the waste as received at the piggeries has been estimated, load for load throughout the year, as: greenstuffs (cabbage, celery, cauliflower, sprouts, &c.), 35 per cent.; bread, 20 per cent.; potato peelings, 30 per cent.; meat, fish, and general leavings from the table, 15 per cent. The percentage of bread is noteworthy, but it should be remembered that the waste comes both from hotels and from private houses.

The sampling of swill for chemical analysis provides very considerable technical difficulties, and we are indebted to Messrs. G. A. Stokes and E. W. Wright, Public Analysts, for the skilful manner in which they carried out this task, and for the actual foodstuff analyses given in Table 1. Each of the six samples analysed by Messrs. Stokes and Wright was a composite mixture of the cooked food taken from six different hand-truck loads at intervals during the feeding-period (3.0 p.m. to 4.30 p.m.) as the swill was being carried to the feeding-troughs.

Selection, housing, and management of stock.—Store pigs are obtained directly from reputable breeders, and are always examined on the farm before purchase. First-crosses between Large White and Large Black, or Large White and Wessex Saddlebacks, have proved the most satisfactory for swill-feeding, attaining bacon-weight some weeks earlier than animals of any other breed or cross so far fattened.

The folly of attempting to feed very young pigs on swill was demonstrated in the early days of the scheme; animals purchased at only 8 to 9 weeks of age either died or failed to gain in weight for several weeks, and the survivors required some 5½ months to attain a marketable bacon-weight. All subsequent purchases have been 14 to 16 weeks old. Such animals, which weigh from 60 to 70 lb. on arrival, begin to put on weight within 7 to 10 days and can be fed to the finishing stage (10-score dead-weight) in from 4½ to 5 months, the average weight increase approximating 1 lb. per day. (In practice, it is generally economic to feed to the maximum weights for which the Ministry of Food pays top price, i.e. 11 score until 16/1/43 and 12 score subsequently.) The condition of store pigs 14 to 16 weeks old has depreciated since 1941. On arrival, the young animals are isolated, observed carefully, and graded into even lots.

The pigs are housed at two centres, viz. the Borough Recreation Ground in Maida Vale, and an 8-acre area of formerly unused grassland at Mill Hill, about 8 miles beyond the borough boundary. The possession of two piggeries proved of great value during the only serious outbreak of disease which has yet occurred. At each centre the piggery is constructed on the same plan and capable of holding about 350 pigs at a time, 8 animals being fattened in each pen. The foundations are of concrete and the 22 ft. square pens are separated from one another by 3 ft. 6 in. wooden fencing. The houses themselves, one in each pen, measure 10 × 10 × 6 ft. and are of wooden construction, complete with

TABLE 1. *Chemical Analysis of the Swill (Stokes & Wright)*

No. of sample[1]	I		II		III		IV		V		VI	
Date of sample	20/10/42		23/10/42		26/10/42		31/12/42		2/1/43		4/1/43	
Water-content	86·20		86·48		89·83		87·22		92·00		88·30	
	Actual sample	*D.M. basis*	*Actual sample*	*D.M. basis*	*Actual sample*	*D.M. basis*	*Actual sample*	*D.M. basis*	*Actual sample*	*D.M. basis*	*Actual sample*	*D.M. basis*
Crude protein	2·56	18·55	2·46	18·20	1·63	16·03	2·19	17·13	1·41	17·62	2·36	20·17
True protein	1·28	9·27	1·20	8·87	0·80	7·86	1·00	7·82	0·63	7·88	1·05	8·97
Carbohydrate	6·79	49·20	7·31	54·07	5·48	53·88	7·20	56·35	4·28	53·50	5·90	50·43
Fat	2·00	14·49	1·44	10·65	1·07	10·52	1·61	12·60	0·90	11·25	1·44	12·30
Fibre[2]	1·00	7·25	0·94	6·95	0·67	6·59	0·68	5·32	0·54	6·75	0·51	4·36
Mineral salts	1·45	10·51	1·37	10·13	1·32	12·98	1·10	8·60	0·87	10·88	1·49	12·74
CaO	0·20	1·45	0·20	1·48	0·16	1·57	0·10	0·78	0·09	1·13	0·21	1·79
P_2O_5	0·12	0·87	0·17	1·26	0·10	0·98	0·12	0·94	0·10	0·75	0·29	2·48

[1] All the samples were taken in the winter months. The make-up and composition might be appreciably different in the summer months, especially in the period when pea-pods and bean-pods might be plentiful in the swill.

[2] The relatively low proportion of 'fibre' is probably due to the high proportion of bread (see page 183).

floors. The troughs are of 9 in. half-round glazed piping. Each run has a slight fall draining directly to a central channel, which in turn leads to a chamber (3 × 3 × 3 ft.) connected with the main sewer. There is thus no passage of liquid matter from one pen to the next.

Feeding is carried out twice daily (8 to 9 a.m. and either 3 to 4 p.m. winter or 4 to 5 p.m. summer), the amount allowed being regulated by the appetite of each group. The average daily consumption throughout the fattening period is about 16 lb. per head, i.e. each pig required a total of about 18 cwt. of kitchen waste from time of purchase to the finishing stage.

The animals are disturbed as little as possible after feeding, and general hygiene is strict, all buckets, feed-trucks, and utensils being cleaned thoroughly after each meal.

Carcass data and quality of bacon produced.—In the early days of the scheme it was sometimes found necessary to transport the animals for long periods by road or rail to the centre to which they had been consigned. This entailed considerable loss, for which the shrinkage allowance was inadequate, but for some time now the pigs have been allocated to a local factory and this has proved much more satisfactory.

Repeated examinations (by C. E. B.) have shown that the meat from the pigs takes the cure well, the distribution of brine being even. Conformation is on the whole good, although by pre-war standards the carcasses are too heavy for No. 1 London grading. The general quality of many of the carcasses appears to be up to pre-war standards for their weight, and well above present-day averages. Although the fat is too soft by peace-time standards (see below), it is not inferior in colour, taste, or firmness to that of any other class of pigs being slaughtered to-day. The even standard of the carcasses is noteworthy and, except when No. 1 Sizable was in plentiful supply, sides of the average quality produced would, in the opinion of C. E. B., have commanded top price in London as No. 1 or No. 2 Heavy during pre-war days.

From two batches of pigs 42 carcasses have been measured by the method of Davidson, Hammond, Swain, and Wright [3]. The back-fat thicknesses have been compared with the expected value of T, obtained by the equation of Callow [4], and, as indicated in Table 2, are considerably fatter than expected. In addition, it should be noted that the mean dead-weight of the animals is considerably above the average of the large series utilized by Callow.

By permission of the Ministry of Food samples of bacon (corner gammon, thick streaky, and long back) have been obtained for examination. The verdict of an experienced 'tasting panel' was that the samples could be graded as follows:

Flavour and colour:	very good;
Saltiness:	mild (very good);
Fat:	soft.

The softness of the fat was confirmed by iodine-number determinations; in the first series so examined, samples of back-fat in the region of the rump (12 animals) were found to have a fat-content of 90·6 per

TABLE 2. *Carcass Data*

	Hot weight lb.	*Shrinkage* lb.	*Net weight* lb.	*Back-fat*					*Length of leg* mm.	*Length of body cavity* mm.	*Calculated value of T (B)*[1]
				A mm.	*B* mm.	C_3 mm.	C_2 mm.	C_1 mm.			
Batch A (12 animals, 19/10/42)											
Range, from	185	4	181	61·5	28·0	39·0	32·0	40·5	24·9	30·2	28·4
to	218	6	212	74·5	53·0	60·5	54·0	58·0	26·4	32·4	33·3
Mean	200·2	4·9	195·3	67·6	39·9	51·1	42·5	47·9	25·7	30·9	30·8
Batch B (30 animals, 28/12/42)											
Range, from	194	—	—	51·8	27·0	40·5	29·5	36·5	—	—	29·7
to	234	—	—	82·0	47·0	62·5	50·5	61·0	—	—	35·7
Mean	215·6	—	—	67·7	34·3	51·5	39·8	46·9	—	—	33·0

[1] From the equation of Callow [4]. The back-fat measurements were taken at (A) shoulder, (B) last rib, and (C) front, middles and back respectively of the muscle of the rump.

cent. and an iodine number of 70, which is at least 10 points too high by normal standards. In an attempt to determine whether or not the animals were being slaughtered at the wrong weight, pooled samples of fat were taken from the 10 leanest, 11 intermediate, and 9 fattest (according to the measurement of back-fat B) of another batch of pigs. The results were:

	Fat	*Iodine number*
Thin (B = 27 to 31 mm.) . . .	93·7	71·2
Medium (B = 32 to 38 mm.) . .	92·3	70·6
Fat (B = 39 to 47 mm.) . . .	94·5	70·7

Within the range of pigs examined, therefore, there would appear to be little justification for slaughtering either earlier or later than at present. As noted elsewhere in the paper, the iodine number of a sample of surface-fat taken from the swill after cooking was only 58·6, indicating that simple removal of such fat might even lead to the deposition of a still softer fat and could in no way improve the hardness of the pigs' fat.

As expected, the fat of the samples tended to render out more than was desirable on cooking, and did not store well. In samples which were stored for 16 weeks at —10° C. the fat turned rancid whereas the lean remained in perfectly good condition.

We are extremely grateful to Dr. E. H. Callow (Low Temperature Research Station, Cambridge) for his advice and assistance in all aspects of the work on carcass and bacon qualities.

Financial aspects.—After deducting capital charges amounting to £324, the trading account for 1941–2 shows a net profit of £2,031. Purchase of pigs amounted to £5,369 and sales to £5,930. In 1942–3 the corresponding net profit was £2,344. Pigs purchased cost £6,939, and sale realizations were £13,096. Over the two years the average net profit per animal was approximately £2 15*s*.

Disease.—During the first two years of the scheme disease has not been a serious factor. At 14–16 weeks of age the stores are not only approaching the end of the critical period of muscle growth [5] but are beyond the danger period of necrotic enteritis and most other post-weaning diseases of the pig, apart from swine erysipelas and swine fever. On arrival, each animal is inoculated with swine-erysipelas anti-serum, and with such treatment only minor trouble from this disease has been encountered. On one occasion a batch of stores was left uninoculated owing to the absence through illness of J. L.; a large percentage of the animals developed the disease, and in spite of energetic serum treatment 2 deaths occurred. The value of passive immunization against this disease must therefore be emphasized. There has so far been one outbreak of swine fever (at the Recreation Ground), and this was dealt with completely before the diagnosis had been confirmed by the Ministry of Agriculture and Fisheries. An emergency-slaughter licence was obtained, and the whole of the stock at this centre disposed of. The number of pigs involved was 330, and although these had cost £1,300 some weeks earlier, they were sold for £1,600, so that the only financial loss was a potential one. It was possible to continue the scheme without

interruption at Mill Hill, and the Paddington centre was in full operation again after a few weeks. The consequences of not dealing promptly with such outbreaks are well known to veterinarians and should be appreciated by pig-owners. Swine fever might not have been eliminated from the premises for some considerable time, cases of ill-health and unthriftiness would have arisen, and casualty pigs would would have been numerous. Eventually, the disease would quite probably have flared up again, perhaps with serious loss. Uncertainty that swine fever has been eliminated is a most disturbing factor, whereas the course adopted in this instance resulted in the premises being closed for 3 weeks only and a fresh start being made without any worry of latent infection.

Any animal which shows the slightest indication of ill-health is isolated immediately, and if necessary is subjected to veterinary examination. A routine veterinary inspection of the whole of the stock is carried out every 4 weeks and has proved of great value. Obscure signs of disease have been detected at an early stage and the appropriate measures taken.

Discussion

As a war-time measure the experiment reported in this paper has been an unqualified success. It remains to be discussed whether or not the system of management can be adapted to peace-time requirements, bearing in mind that in the immediate post-war years the importation of animal feeding-stuffs may remain at a low level. The problem of collecting and dealing with swill is much more complex in a municipality than in a camp or institution, although it appears to have been dealt with during peace-time in many American cities, including Los Angeles, which for many years has supplied 400 tons of swill daily to the largest pig-farm in the world, that at Fontana, California [6].

The first essential in the prosecution of such schemes is the co-operation of the residents in separating the potential pig-food, since the sorting of edible from non-edible refuse after collection would not suffice. That voluntary separation would be effected in peace-time is doubtful, and it would therefore appear necessary that some form of compulsion be enforced.

Granted a supply of suitable swill, it would be necessary in the case of a Metropolitan Borough to relate pig-keeping to a normal statutory duty of the authority, e.g. the collection and disposal of kitchen waste. The Ministry of Health has power to stop local authorities from exceeding their statutory duties by surcharging the members with any illegal expenditure. In war-time no objection has been raised by the Ministry against pig-keeping, quite apart from the fact that it has shown a profit. If, in peace-time, kitchen waste had to be paid for at a high cost (and it must be remembered that hotel refuse could be sold to contractors in the pre-war years), a sharp fall in bacon prices might entail a loss with which—if statutory authority for pig-keeping were not given—it would be open for the Minister to surcharge the members of the Council. These difficulties have been emphasized, but we have little doubt that in practice the only real obstacle would be the failure of householders

and hotel keepers to separate their refuse into edible and non-edible portions, and that if this were overcome the financial results would be likely to remain very favourable.

The other main consideration is the market open for pigs fed largely on swill. The evidence accumulated in this paper leaves little doubt that carcasses resulting from swill-feeding alone, whilst suitable enough for the 'Midland' pork trade, and also for the manufacturers of sausages and 'small goods' in London and throughout the country, would not satisfy producers of the best-quality bacon. It seems probable that after the war light weights will again be in demand for 'Wiltshire' style bacon, in which case there is no evidence that the entirely swill-fed pig of suitable weight would be able to compete with the largely meal-fed animal in respect of carcasses and keeping-quality. In war-time bacon is distributed with a minimum of curing and is probably consumed within a few days of purchase: these procedures will almost certainly be altered in post-war years.

It would appear necessary, therefore, to modify in some way the all-swill ration. Experiments to determine what form of balancing meal could be utilized might well be conducted even in war-time, and might furnish an indication of the optimum finishing weight, which would probably be heavy.

The pre-war imports of pork were heavy, and there seems every reason to suppose that the post-war market will absorb all the pork which is produced at home. This is an important point in favour of swill-feeding, and from the municipal point of view the probable financial success of the enterprise, the production of manure, and even the educational value of having farm animals within the borough, are all of importance. The proximity of the London market, the requirements of which for 'small goods' production are not so exacting as regards quality as in the case of the 'Midland' style bacon trade, is valuable to London boroughs.

We have not attempted to compare fresh-boiled with 'processed' swill, but we feel that, whenever the food can be utilized within the locality in which it is collected, and stringent precautions be taken against disease, it is quite unnecessary to go to the expense of processing.

Summary and Conclusions

(1) A description is given of a municipal pig-fattening scheme, which has been introduced as a war-time measure, and in which the sole foodstuff used is household swill.

(2) It has been found possible to produce over 350,000 lb. of pig-meat per annum from the swill collected within the borough (200 tons per month); the approximate annual net profit to the municipality is £2,250 or about £2. 15*s.* per pig fattened.

(3) The quality of the bacon produced is above the war-time average for all classes of pigs slaughtered at the regional factory, and is considered to be markedly superior to that from swill-fed pigs which were slaughtered at the same factory before the war. It is of very good flavour and colour, and of mild saltiness, but contains soft fat.

(4) Analyses of the surface-fat of the swill after cooking, and of the body-fat of pigs of different degrees of fatness, indicate that it would not be possible to reduce the softness of the body fat either by simple processing of the food or by slaughtering the animals at other weights.

(5) Emphasis is laid upon care in the collection and treatment of the swill; hygienic and uniform management; routine veterinary inspection and resolute measures against disease; above all, selection of animals of suitable age and breed for fattening on such a diet. Store-pigs (of which first crosses of Large White × Large Black and Large White × Wessex Saddleback have been found the most satisfactory) should be well started on the farm, and never brought to swill-feeding before at least the 15th week of life. The possibility of continuing this type of management in post-war years is discussed.

(6) Modification of the all-swill ration will probably be essential if municipally-produced bacon-pigs are to compete with other categories in peace-time. Experiments to determine what form a 'balancing meal' should take, and to what weights the pigs should be fattened, are desirable.

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BEEF CATTLE IN PEACE AND WAR

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Introduction.—In time of war it is necessary for every nation to determine the total amount of each important food constituent contained in the total supply of food which, whether by production within or by importation, is available for the subsistence of its population. And the home production of food, which is the business of agriculture, must be examined in order to ensure that the land, the available fertilizers, farm machinery, and labour are used in such a way as to produce the largest possible amounts of the most necessary human foods.

A rising standard of life resulting from an increasing productive power per man, i.e. an increase of real wealth, is universally associated with an increased consumption per head of animal products, milk, eggs, and meat of all kinds. And it is well known, though the implications of the fact are not always, even not generally, realized, that the production of such human foods of animal origin is expensive, indeed wasteful, in that the feeding-stuffs consumed by the animals from which they are derived are always greater, and often very much greater in mass than the amount of human food secured. Where, as in the case of poultry or pigs, much of the animal's food could in fact be eaten by man in its original form, only a great improvement in value can counterbalance the loss of mass.

It is therefore necessary to determine how far each food of animal origin possesses qualities which cannot more economically be secured from vegetable sources, and to evaluate it in terms of the amounts of food substances, proteins, fats, carbohydrates, vitamins, and minerals, which can be secured from each gallon of milk, single egg, or the body of an individual animal.

For milk we have abundant analyses, for meat far fewer. And for the variation of the yield of a single joint of meat per pound, and for the yield from a single complete animal, we have so few data that it is difficult to make any reliable estimate of the amount of human food of every kind which we may expect to secure from the cattle, sheep, and pigs now being fed in Britain. In view of this uncertainty it is evident that we cannot determine with any reliability the efficiency with which these animals convert their feeding-stuffs into materials edible by man.

The few scattered analyses of beef cattle, usually of undefined character, made for example by Wood and Newman [1], provide a singularly slender basis for discussion, and an investigation of the literature, summarized very well indeed by O. G. Hankins and H. W. Titus [2], shows that no successful attempt has yet been made to reduce the recorded analyses of beef cattle to a form which will allow the value of an individual beef steer as human food to be estimated by calculation from simple qualities.

It is obvious, from the tables and graphs in Hankins and Titus's

summary, that the changes in composition of beef carcasses are systematic, and should hence be capable of expression by equations or by curves, so that if sufficient and sufficiently varied data were available the solution of the problem should be a simple, if laborious, matter.

The first to determine the chemical composition of the whole body of an ox and of its edible portions were Lawes and Gilbert, who in September, October, and November 1849 killed, dissected, and chemically analysed a calf, a half-fat Aberdeen steer, and a fat Aberdeen ox. Their paper [3], published by the Royal Society in 1859, is remarkable for the insight it shows into the character of the information needed and the ways it can be applied for a further understanding of and improvement in farming practice. For some sixty years no one repeated Lawes and Gilbert's work, but there were innumerable feeding trials, in which a steer of known weight was fed on known amounts and qualities of food until it reached some higher weight and was then slaughtered.

The composition of the animal at the beginning of the experiment was expressed by some such phrase as 'a 700 lb. store, 24 months old in poor condition', and at the end of the experiment it was a fat bullock, weight 1,000 lb., killing out at 58 per cent. and with a market grade *x*. In these experiments the quantities by which the progress was measured were guessed, only the extraordinary skill of some butchers or farmers in estimating quality and weight of beef steers rendered the results of any value.

It is clear that the discovery of any practicable method of determining in quantities of chemical substances the materials contained in a steer and the proportions of these substances which are edible by man would greatly enhance the value of all feeding trials.

The wish to determine such a method led two groups of American workers simultaneously in 1908 to begin experiments in which large numbers of cattle were fed and slaughtered. In these experiments, as in those of Lawes and Gilbert, the animal is weighed, killed, and weighed again, giving live- and dead-weights. It is then bled, skinned, and cut up, and the blood weighed. The urine in the bladder and the contents of the digestive tract are removed and weighed, this weight of the fill, subtracted from the live-weight, gives the empty body-weight, which is sometimes, though seldom, of value. The cutting up of the body must be done essentially as a butcher proceeds, the 'carcass' which contains the larger part of the edible materials being separated from the edible and inedible offals, and each part weighed separately. The carcass is subdivided into customary parts and then into 'joints', and then each section is dissected, the 'fatty tissue' (the fat of the butcher and housewife), 'lean flesh', and bone being separated from one another and from tendons, blood-vessels, &c. Finally every part must be minced up and samples taken for chemical analysis, which must at the least determine water by drying, fat as the materials soluble in ether or other fat solvent, and protein either by direct determination of nitrogen, or by difference. The ash (mineral matter) must be determined, and for some purposes calcium and phosphorus estimated in it.

Dr. Haecker of the University of Minnesota in 1908 conceived impor-

tant additions to the original investigation and began a great experiment of which an account was published in 1920 [4]. The important innovations introduced by Haecker were that he realized that much further information of great potential value would be obtained by raising a large number of animals from birth, determining the actual daily food consumption of each individual, and slaughtering animals which seemed to represent the average character of the herd at regular intervals, in his case at each 100 lb. live-weight from 1 to 14. Each animal was dissected and chemically analysed, and the foods eaten were controlled by the ordinary methods of agricultural chemists.

It is an unfortunate fact that the data from this experiment, which was certainly well designed and to all appearance most accurately carried out, have never been published in a form which allows them to be used. It is particularly unfortunate that they are largely presented in the form of averages, usually of 4 individuals. As two individual steers of 700 lb. live-weight may differ by 300 per cent. in their yield of human food measured in energy units, it is evident that averages may be entirely misleading.

Haecker used a unit of energy value, the 'organic product', which is really the sum of the amount of protein added to the amount of fat multiplied by 2·25, contained in the body or any part of it. The figure is in effect the weight of an unspecified carbohydrate which is equivalent in calorific value to the object evaluated. The unit is a very convenient one, because, being a weight, it can legitimately be expressed as a percentage of any other weight, and I use it largely in the rest of this paper. Following, or perhaps preceding Haecker, Moulton, Trowbridge, and Haigh [5], of the University of Missouri, undertook a similar but more elaborate and even better experiment designed by Dr. H. J. Waters. They fed 62 calves from shortly after birth and slaughtered samples at intervals of days and not of weights, dissecting and analysing them. From the first they divided these animals into three groups and some specially treated individuals.

The animals of Group I were fed all that they would eat of a diet which consisted essentially of one-third hay and two-thirds of a grain mixture of standard composition.

Group II received an identical diet in smaller amount, which secured normal or nearly normal growth without much fattening.

Group III received the same diet (which may have been rather small in bulk) in still smaller amount so as to lead to definite restriction in growth. The amount eaten must have been very nearly the smallest possible, for up to a weight of about 1,000 lb. the fat in the entire body never exceeded the low level of 10 per cent., and several steers died. All the animals were steers of beef character, mostly Herefords or Shorthorns or a cross between them.

These experiments were, so far as can be judged by the published record, of the highest quality, and the data were published in a most convenient form and with an illuminating discussion [5]. The assumption underlying them is that beef steers of similar genetic character, when fed in the same place in the same way, will follow identical paths of development, and that an animal slaughtered at any given time and

weight will show the character of all its fellows which live on to be slaughtered later at higher weights.

In both the Minnesota and Missouri experiments this assumption was tested by slaughter of more than one individual at the same stage from a group which had received identical treatment. The results justify the assumption.

We can therefore use the ascertained composition of animals slaughtered at different stages, which belong to the same feeding group as if it had been in fact determined (as it cannot be) for a single individual, at various stages of its life history. Much later in 1941 the need to determine accurately the quantities of human food which were yielded by cattle of various kinds when slaughtered led Drs. Callow and Hammond, of the University of Cambridge, to slaughter, dissect, and analyse 20 cattle bought from ordinary markets, but carefully selected so as to represent common types of calves, stores, fat steers and heifers, cows and bulls. This work is expected to be published shortly.

It was originally intended that the present paper should have formed part of a larger work in which the data for the Cambridge cattle were discussed in association with the published American figures. But it has proved more convenient to divide the whole into parts, of which this is the first, which will be followed by an account of the Cambridge work. But I wish to make clear that throughout my own calculations I have been in constant touch with Drs. Callow and Hammond and that I owe very much to them, not only for criticism, but especially because they gave to me much practical wisdom derived from a most extensive practical familiarity not only with the carcass and meat, but with the whole organization of the beef-cattle industry in Great Britain.

It may be said that the Cambridge data confirm and greatly extend the conclusions I have reached about the yield of human food from steers; they show that to all appearance heifers are essentially identical with steers in this respect, whilst cows and bulls differ.

I. *The Dietetic Qualities of Beef*

The human foods derived from the bodies of cattle are 'beef', fats ('suet' and 'dripping'), which come not only from the carcass but from the offals, and edible offals not 'fat' (such as liver, heart, tongue, kidney) which form a relatively small part of the whole.

Physiologists in general tend to regard beef as predominantly a source of high-quality protein and to ignore many of its other qualities. Ordinary people eat beef because they like its flavour, say that it gives them energy, and is a lasting food, delaying the onset of hunger after a meal.

Protein.—The protein in beef comes almost entirely from skeletal muscle, which is of relatively constant composition, and is calculated on the weight of the muscle freed completely from fat; the protein forms about 21 per cent., the rest being mainly water. Its value in a human dietary is unquestioned, but it can be replaced by any other protein from an animal source (e.g. milk), or by suitable mixtures of vegetable proteins. The food material present in the largest amount in the carcass of

a good quality steer is, however, not protein, which accounts for only 10½ per cent. of the carcass weight, but chemical fat which in such animals forms 25 to 35 per cent. of the carcass.

The calorific value of fat is so high, 2·25 times that of protein for any given amount, that the energy value of beef is determined very largely by its fat-content.

Fat is of great importance in any human diet, especially to men in temperate and cold climates, and perhaps to those who live in hot deserts. Judged by its energy value, pure fat is by far the most concentrated form of food known, and enables the necessary amount of 'calories' to be eaten in the minimum weight and volume, so that the meal can be less bulky. Indeed, it is impossible for most men using 4,000 calories or more per day to meet their needs on any diet which does not contain a considerable proportion of fat.

The demand by men in heavy work, e.g. miners and farm labourers, for additional supplies of meat when further considered is often found to be met in peace-time by fat bacon, of which the fat-content is 20 times that of protein. Thus far from being unimportant the fat-content of meat is of the greatest significance. Fat has the important quality of delaying the process of digestion, and by keeping food in the stomach for a longer time than would be the case in its absence, staves off the feeling of hunger. Some small amount of fat containing the lower unsaturated fatty acids, oleic, linoleic, and arachidonic, is an obligatory part of every diet, but there is no reason to suppose that it cannot be supplied from vegetable sources.

Vitamins.—The vitamin-content of beef (excluding liver and perhaps other offals) is very small, only in the case of nicotinic acid, and perhaps riboflavin, do substantial proportions of the necessary daily intake come from beef in a normal British diet.

Minerals.—The mineral-content of beef is very small; it is poor in calcium, and the relatively large amount of iron contained in it is in a form in which it is usually held to be unavailable to man.

Thus the value of beef depends on the psychological effect of the pleasure derived from eating it, and on the protein and fat it contains; and the value of the human food derived from a beef animal can be expressed in terms of weight of protein, of its yield of calories when oxidized, and by the results of tasting tests.

In peace-time fats are abundant so that it matters little how much is contained in beef, and that food may legitimately be valued as a source of protein, and especially for its appetizing value. This aesthetic quality is in fact associated with the presence of a considerable amount of fat, not only in fatty tissue but as the marbling fat lying between muscle fibres in lean meat. [The optimum fat-content has been determined by the Cambridge investigators.] But in war the supply of fats is difficult and the value of the fat contained in beef animals is much enhanced; under these circumstances it is therefore desirable, if it can economically be done, to produce carcasses which are fatter than would usually be preferred in peace-time. And under war conditions economically means to an even greater extent than in peace the use of the smallest

possible quantities of feeding-stuffs for the production of a given amount of human food.

The matter is further discussed in Section V, but it is necessary for our purposes to evaluate both carcass and whole body in terms of protein and of calorific value, because the latter is the only expression which will bring protein and fat into the same figure and allow comparison with feeding-stuffs similarly expressed.

II. *The Composition of the Whole Body*

Any inspection of analytical figures shows that the most variable constituent in the body is fat. It follows that the first stage is to deter-

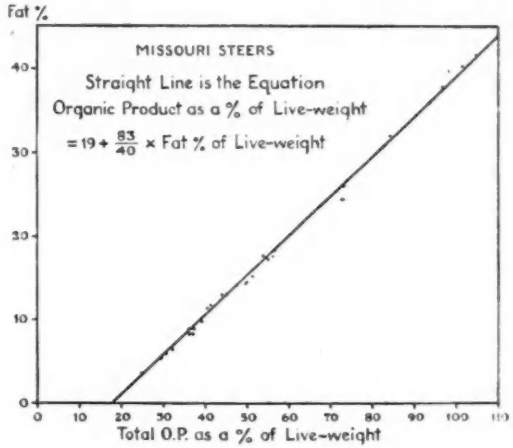
Fat %
MISSOURI STEERS
Straight Line is the Equation
Organic Product as a % of Live-weight
= 19 + 83/40 × Fat % of Live-weight
40
30
20
10
0
0 10 20 30 40 50 60 70 80 90 100 110
Total O.P. as a % of Live-weight

FIG. 1.

mine how far the composition of the body and its other qualities are related to the fat-content, most usefully expressed as a percentage of the live-weight.

Energy value of body.—If, as in Fig. 1, the total 'organic product' (a measure of calorific value) of the whole body of the Missouri steers, expressed as a percentage of the live-weight, be plotted against the amount of fat in the whole body also as a percentage of the live-weight,[1] it is found that the points representing individual animals fall so closely on a straight line that it is unnecessary for our present purely practical purpose to apply any refined test of goodness of fit.

The regression equation determined graphically is:

Total Organic Product as a percentage of live-weight $= 19 + \frac{83}{40} \times$ Fat% of live-weight.

Protein-content of body.—If the total amount of protein in the body, which of course includes that in the hair, skin, and bones, as well as all

[1] This procedure is justified by the wide range in character found amongst experimental animals of similar live-weights.

other tissues, expressed as a percentage of live-weight be plotted against the percentage of fat (Fig. 2), it is found that the points representing the individuals of the Missouri experiment have a wide scatter, but that they tend to fall as the percentage of fat rises.

It is therefore evident from the scatter that factors other than fatness influence the percentage of protein contained in the body. It is, for

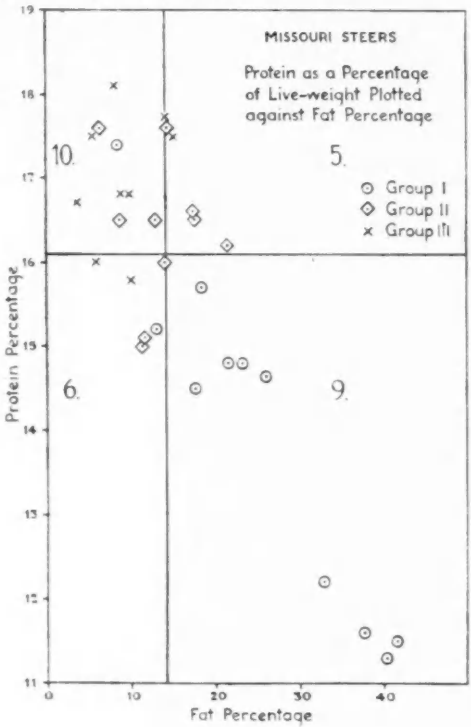

FIG. 2.

example, obvious that the animal's shape, whether it be narrow from side to side or more rounded in section, alters the area of the skin for any given live-weight. It is at present difficult to find any expression for these other factors, which probably involve amongst other things the rate of growth, which Dr. Hammond has shown greatly to influence the proportions of an animal.[1]

The total variation in protein percentage is very considerable; it varies from 11·3 to 18·1. If the amount of protein be expressed as a percentage of the live-weight less the total fat-content, which is a measure of the

[1] The equation Protein as per cent. of live-weight = 18·6 − (Fat per cent. × 1·81), gives results which may be 10 per cent. out, with an average deviation of 4·35 per cent. These deviations are in part related to age, but the steers in Group I show no such correlation.

actual living materials in the body, and this be plotted against the percentage of fat then it will be seen in Fig. 3, which represents Dr. Haecker's Minnesota steers, that the scatter is smaller and the influence of fatness more obvious. This is in part due to the homogeneity of these steers, which in general were fed to appetite. I regret, however, that

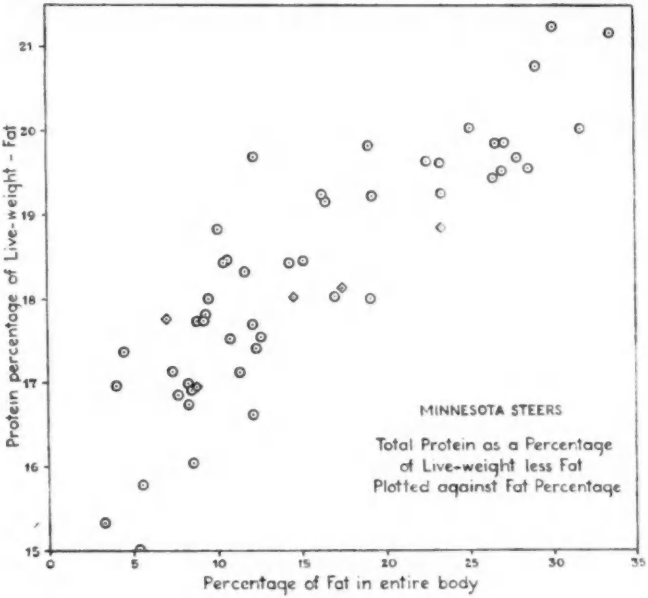
Protein percentage of Live-weight - Fat
Percentage of Fat in entire body
MINNESOTA STEERS
Total Protein as a Percentage
of Live-weight less Fat
Plotted against Fat Percentage

FIG. 3.

I have been unable to find a mathematical expression to represent the protein-content of an individual steer with a usable accuracy.

III. *The Yield of Human Food*

The amount of human food which can be obtained from each steer of the Missouri experiment can be derived from the published figures, and I have determined it for two different assumptions.

During war-time, when the supply of fats is difficult and important, it seems evident that all the offal fats are edible, or can at any rate replace vegetable fats that can be made into margarine or cooking oil and utilized in the manufacture of soap or for other industrial uses. I have therefore calculated this amount; but in peace a part of the offal fat is not eaten, so that as an alternative I have also calculated the yield of human food from the carcass together with the tongue and some other edible offals, which collectively amount to very little.

Amount of human food in body.—If, as in Fig. 4, we plot the amount of human food in both carcass and offal calculated as Organic Product (that is on an energy basis) expressed as a percentage of the Total

Organic Product in the whole body, against the percentage of fat, we find that the points representing the Missouri steers all fall closely about a curve whose equation, determined graphically from a plot on logarithmic paper, is

$$\% \text{ Edible} = \frac{\log \text{Fat } \% - \log 10}{0{\cdot}02076} + 59.$$

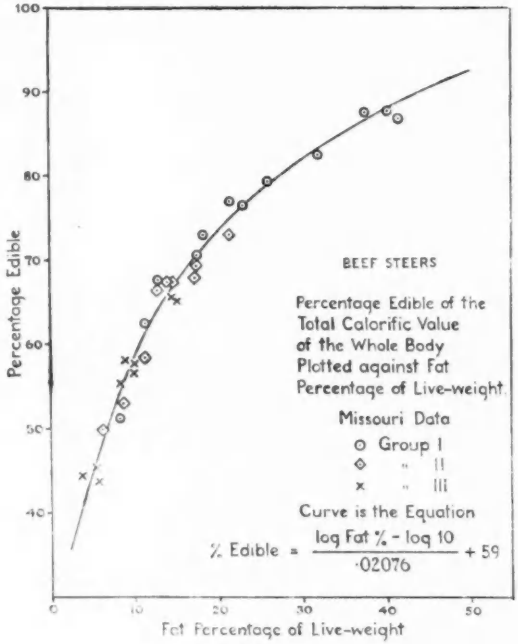
Percentage Edible
Fat Percentage of Live-weight
BEEF STEERS
Percentage Edible of the Total Calorific Value of the Whole Body Plotted against Fat Percentage of Live-weight
Missouri Data
Group I
" II
" III
Curve is the Equation
% Edible = log Fat % - log 10 / ·02076 + 59

FIG. 4.

The corresponding equation for the percentage edible contained in the carcass is

$$\% \text{ Edible in carcass} = \frac{\log \text{Fat } \% - \log 10}{0{\cdot}02551} + 51.$$

We have already determined an equation which represents the Organic Product of the whole animal as a function of the percentage of fat. Multiplying this by the figure expressing the percentage which is edible we obtain the equations:

Edible Organic Product of carcass and offal as a percentage of live-weight

$$= \left[19 + 83\left(\frac{\text{Fat } \%}{40}\right)\right] \times \left[\frac{\log \text{Fat } \% - \log 10}{0{\cdot}02076} + 59\right],$$

Edible Organic Product of the carcass as a percentage of live-weight

$$= \left[19 + 83\left(\frac{\text{Fat } \%}{40}\right)\right] \times \left[\frac{\log \text{Fat } \% - \log 10}{0{\cdot}02551} + 51\right].$$

These equations are represented in Figs. 5 and 6 respectively with the individuals of the Missouri experiment plotted on to them. In the first case the yield of carcass and offal in energy terms is expressed with an

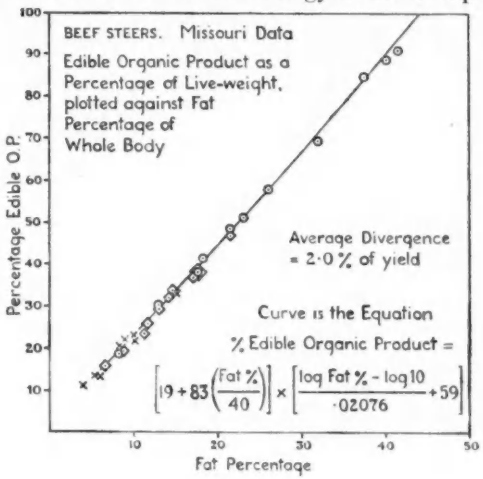
BEEF STEERS. Missouri Data
Edible Organic Product as a Percentage of Live-weight, plotted against Fat Percentage of Whole Body
Average Divergence = 2·0 % of yield
Curve is the Equation
% Edible Organic Product =
$\left[19+83\left(\frac{\text{Fat \%}}{40}\right)\right]\times\left[\frac{\log \text{Fat \%}-\log 10}{\cdot 02076}+59\right]$
Percentage Edible O.P.
Fat Percentage

FIG. 5.

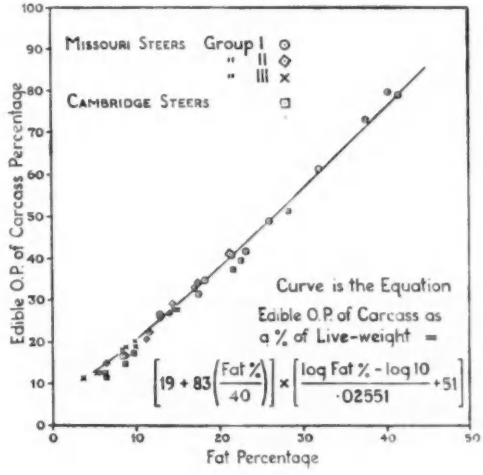
MISSOURI STEERS Group I ⊙
" II ◇
" III ×
CAMBRIDGE STEERS □
Curve is the Equation
Edible O.P. of Carcass as a % of Live-weight =
$\left[19+83\left(\frac{\text{Fat \%}}{40}\right)\right]\times\left[\frac{\log \text{Fat \%}-\log 10}{\cdot 02551}+51\right]$
Edible O.P. of Carcass Percentage
Fat Percentage

FIG. 6.

average deviation of 2·0 per cent.; in the second the yield of the carcass, the fit, though good, has not quite so high an accuracy.

As the range in yield of steers weighing 700 lb. varies 300 per cent., it is evident that these equations are adequate for any practical purpose, and they are indeed remarkably good for any biological data.

Human food in any steer.—It follows from the nature of these equa-

tions that the yield of human food measured in calories is directly proportional to the live-weight for beef steers of any given percentage of total fat, and that at any given weight the yield of human food by a beef steer is related to the percentage of fat, an increase of which by 1 gives steadily increasing yield as the percentage of fat rises from its minimum, about 3·0 per cent., to the maximum, which exceeds 40 per cent.

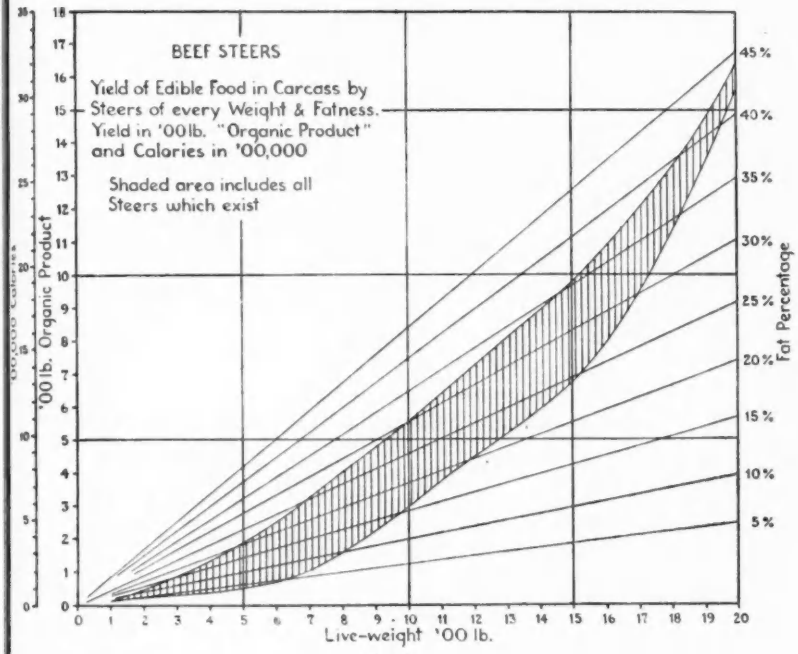

FIG. 7.

These facts are represented in Fig. 7, in which the intersection of the oblique lines representing steers of a definite percentage of fat-content with verticals representing live-weight, gives when read horizontally the yield of human food from the carcass in calories or lb. of organic product. On this graph there appears a shaded area within which all the analysed steers known to me fall and which must include nearly all steers which can exist.

The form of this area depends on the following facts:

Size of steers.—The maximum size that can be reached by steers can be measured by subtracting the total amount of fat in the body less that small proportion, the 'element constant', which forms part of the mechanism of the living cells, from the live-weight, plotting the amounts so calculated against age and determining the value to which the curve becomes asymptotic.

For the Missouri steers this maximum rises with the rate of growth.

Steers of Group I, which over their whole life made live-weight gains up to 1,000 lb. exceeding 2 lb. per day and even at 1,900 lb. of 1·35 lb. per day, approached a maximum live-weight less fat of 1,200 lb. Group II, which up to 800 lb. made live-weight gains of 1 lb. per day, falling to 0·79 lb. at 1,250 lb., approach a maximum live-weight less fat of 1,000 lb., whilst Group III, which made gains of from 0·62 to 0·81 lb. per day, approach a maximum of 880 lb. live-weight less fat. These differences are obviously related to alterations in the actual size, and especially in the proportions, of the skeleton.

These changes depending on the level of food-intake are vividly shown in the graphs published by Moulton, Trowbridge, and Haigh [5, 1], from which it appears that whilst height at hips or withers is comparatively little affected, the length of the body, the width at the hips, and especially the girth at the heart, are all greatly reduced by reduction of the amount of food eaten per day.

The general stunting effect of food restriction is, of course, familiar; it is well shown by comparison of a Victorian human group in England with an equivalent group to-day. From these considerations it follows directly that the excess of weight of any beef steer above 1,200 lb. must be due to accumulation of stored fat, and that very large animals of, say, 1,800 lb. live-weight (for Herefords or other breeds of similar size) are inevitably very fat, containing at least 600 lb., a percentage of 33.

Thus the difference in yield of human food between the fattest and the thinnest steer of any given weight when measured as a percentage of that of the thinnest, becomes progressively smaller as the live-weight increases from 700 lb. to its maximum of about 2,000 lb.

Appetite.—The maximum fatness possible at any weight is conditioned by the limitation set by appetite, which is determined by the weight of dry matter contained in the meal, and not by its total mass, so that concentrated foods (e.g. grain) allow more digestible food to be eaten per day. The amount of digestible food required for maintenance, to meet the necessary muscular movements of the vascular system and for breathing, &c., has a first call on the available food supplies, and its amount per lb. live-weight is less the greater the live-weight of the animal.

The remaining food can be used for growth, i.e. for increase of the live-weight less fat, or for storage of fat. Of these, growth has priority.

As growth slows down when the maximum size is approached, and ultimately effectively ceases, it is clear that it becomes progressively easier to fatten an animal as it grows larger. That is, a small animal, a yearling, can be fattened to a high level only by feeding it on a diet containing a very high proportion of concentrates. And even so it can be done only with high-grade beef cattle whose appetite is very great.

It is possible that some American 'creep-fed' steers may actually lie above the limit set by Fig. 7 in the region of 500–700 lb.

Edible protein in a steer.—As I have been unable to design an equation to express the total amount of protein in the body of a steer, I cannot calculate the amount of protein edible by man which it will yield by determination of a formula analogous to that for edible O.P., and

all that can be done is to plot individuals and thus quite empirically arrive at some conclusion. This is done in Fig. 8, inspection of which shows that the edible protein in the body expressed as a percentage of live-weight is comparatively constant, no matter what the live-weight may be: it is in the neighbourhood of $8\frac{1}{2}$ per cent. But fat animals, the individuals of Group I, have systematically a lower yield than those

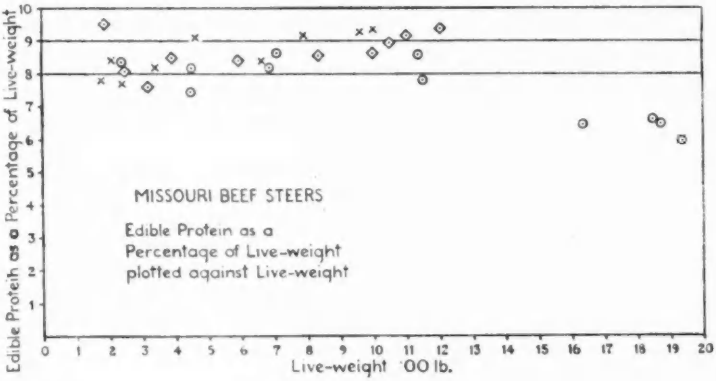

FIG. 8.

which have been less intensively fed, and those of Group III, starved and of low fat-content, have a higher yield than normal. In that the percentage of protein in fat-free muscle is very constant, this result is in no way unexpected. So many factors influence the amount that it is as yet impossible to produce an equation which will take all of them into account.

Killing-out percentage.—As the total fat-content of the body is determined only by a most laborious process, it is desirable to investigate the possibility of estimating its amount by some more practical method, especially by one which could be applied by butchers in the ordinary course of trade. The one figure regularly determined is the dressing or killing-out percentage, the proportion of the live-weight represented by the cold carcass. This figure forms the basis of the quality grading of beef cattle in Great Britain; as it increases, so does the price paid per live cwt.

J. L. Lush in a most valuable paper [6] has dealt with the published figures of all beef animals which have been analysed and has shown that the dressing percentage is a linear function of the percentage of fat to live-weight. He derived the regression equation:

$$\text{Dressing percentage} = \frac{\text{Fat \%} + 86{\cdot}40}{1{\cdot}784}.$$

But the correlation coefficient is only $+0{\cdot}8460$, from which it follows that factors other than the degree of fatness influence the figure observed, and that their joint effect may be so great that the formula has comparatively little practical utility.

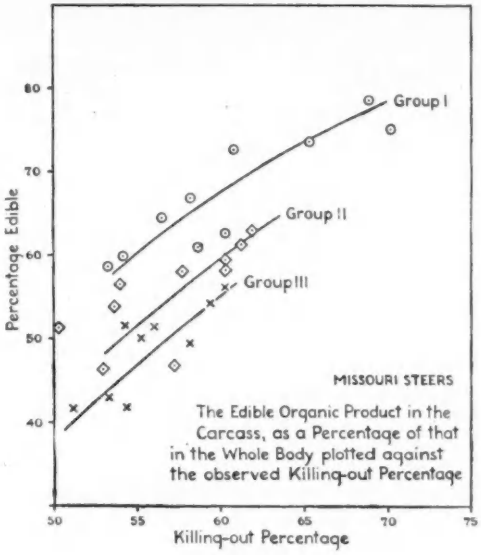
Group I
Group II
Group III
MISSOURI STEERS
The Edible Organic Product in the Carcass, as a Percentage of that in the Whole Body plotted against the observed Killing-out Percentage
Percentage Edible
Killing-out Percentage
80
70
60
50
40
50
55
60
65
70
75

FIG. 9.

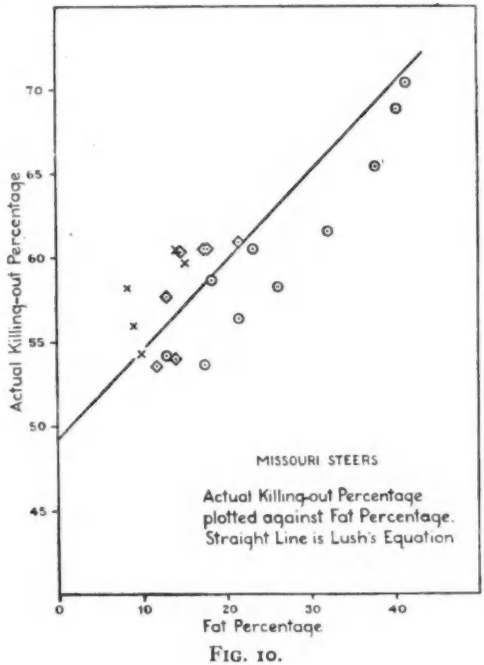
MISSOURI STEERS
Actual Killing-out Percentage plotted against Fat Percentage. Straight Line is Lush's Equation
Actual Killing-out Percentage
Fat Percentage
70
65
60
55
50
45
0
10
20
30
40

FIG. 10.

To check this fear by a practical test we may, as in Fig. 9, plot the edible Organic Product of the carcass expressed as a percentage of that in the whole body against the observed killing-out percentage. Were the killing-out percentage completely correlated with that of the fat

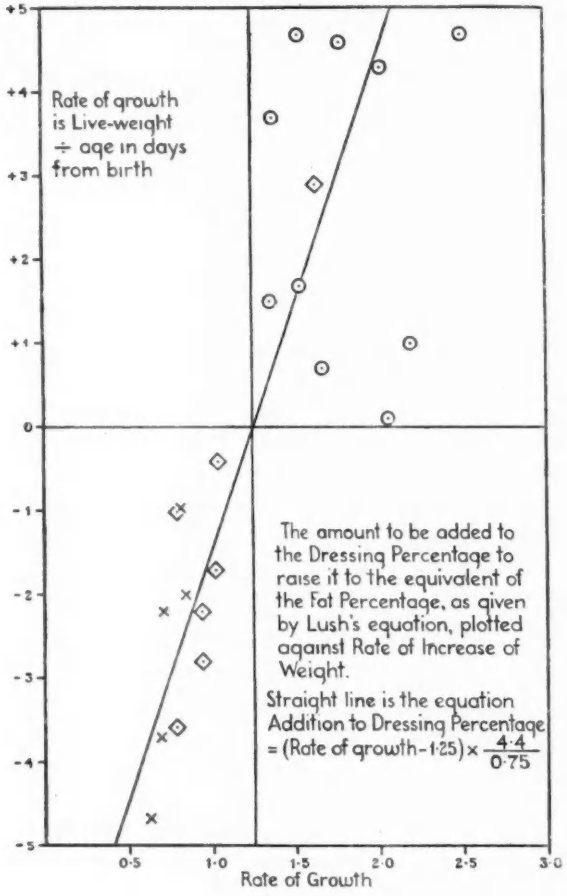

FIG. 11.

we should obtain a graph similar to Fig. 4 with the points a little less closely grouped round the curve. In fact, the individuals of the three groups lie in separable areas, those for each group being related, though not closely, to a separate curve.

If (Fig. 10) we plot the actual killing-out percentage against the percentage of fat in the whole body, and superimpose a straight line representing Lush's regression equation, we can determine by measurement the extent to which the real dressing percentage of each animal

exceeds or falls short of that which would be expected from the percentage of fat, were the correlation between the two ratios complete. The divergence is very considerable: it amounts on the average to 2·59, to be added to or subtracted from the recorded figure.

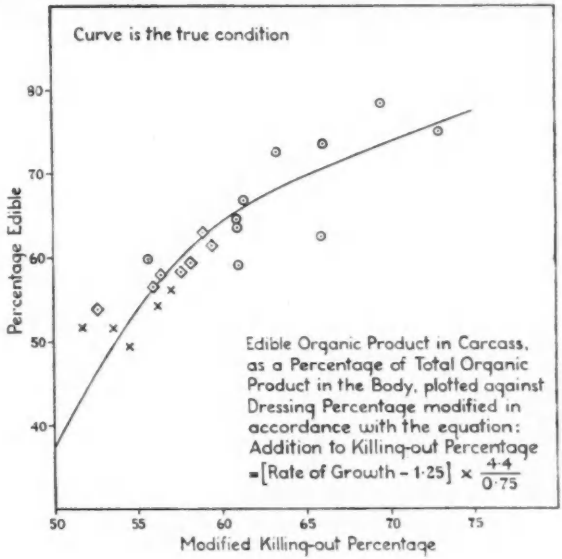

FIG. 12.

The general run of the figures suggests that 'rate of growth' is one of the important factors, and that this can be investigated by plotting the deficiency or excess against the rate of growth in lb. per day determined by dividing the live-weight at death, less a conventional birth-weight of 80 lb., by the number of days from birth. The result is the graph in Fig. 11, p. 205, from which it is obvious that as lines parallel to the base lines through *O* and a growth-rate of 1·25 lb. per day leave all the points in opposite quarters, there is a genuine effect of growth-rate on the dressing percentage actually achieved.

If we draw a straight line through the cross-point so as to divide the points equally and treat this as a regression equation we obtain the formula:

Addition to be made to observed killing-out percentage = (Rate of growth $-1{\cdot}25) \times \frac{4{\cdot}4}{0{\cdot}75}$.

The effect of such a modification may be tested by plotting the corrected killing-out percentage against that of the fat. The scatter of the points is thereby greatly reduced, so that the average divergence becomes 1·66 instead of 2·59.

The actual effect of this treatment can be illustrated, as in Fig. 12, by repeating Fig. 9, but using the modified version of the dressing per-

centage. In it the whole population is visibly approaching the single curve which is the true expression of the conditions.

Thus the effect of rapid increase in weight resulting from heavy feeding is to increase the proportion of the calorific value of the body which is included in the edible parts of the carcass. In other words, a beef steer of a given weight and killing-out percentage yields much more human food, measured in calories, if it be fed at the highest possible level than it does if produced at a lower rate of food consumption.

This means that the use of the killing-out percentage in determining price levels, unless modified by a weight-for-age factor, may tend to discourage rapid feeding, which we show later to be the way of treating beef steers that is most economical in foodstuffs.

IV. *The Cost of Growth and Fattening*

The purpose of agriculture in war-time is to produce the maximum possible amount of human food of designated character with the smallest possible consumption of feeding-stuffs, other materials, and labour. This simple aim is, however, in practice difficult to determine; if the human food needed be beef, then the way of producing it which is most economical in feeding-stuffs, judged by the digestible energy and protein consumed, may not be desirable or even possible, because although coarse fodders and roots may be abundant, concentrates, a high proportion of which in the diet may be desirable on simple theoretical grounds, may in fact be unprocurable.

Further, beef cattle produce farmyard manure, and although this only represents an addition to the manurial salts on the farm in so far as they are derived from purchased food, the redistribution of them from one part of the farm to another, which is brought about by keeping animals, may be of great practical importance. Also the organic matter in dung is for some soils of paramount value, and such alternative modes of supplying it as the ploughing up of old pastures or temporary leys may be less convenient.

The data of the Missouri experiment are so complete, and the experiment was so well designed, that many important conclusions can be drawn from them. The human food produced by those cattle that were analysed is known in the accepted form of pounds of protein and calories of energy (see Section III).

The evaluation of the food which they consumed is much more difficult. The amounts of milk, hay, and standard 'corn mixture' which each ate is recorded for 30-day intervals over the whole life, and from the results of chemical analyses the amounts of protein, fat, nitrogen-free extract, crude fibre, and ash have also been stated for 30-day periods. But the animal is unable to digest all these materials completely, and to discover how much of them pass into the body it is necessary to apply a digestibility coefficient to the analytical figures.

I have preferred to apply American figures [7] for the digestibility of each food to the amounts eaten and thus determine the amounts of digestible protein, and digestible energy available over the whole life from birth, making a conventional allowance of milk to cover the period

between birth and the entrance to the experiment. The digestible energy so valued is the 'total digestible nutrients', commonly used by American workers. It is necessarily greater than the starch equivalent used in this country.

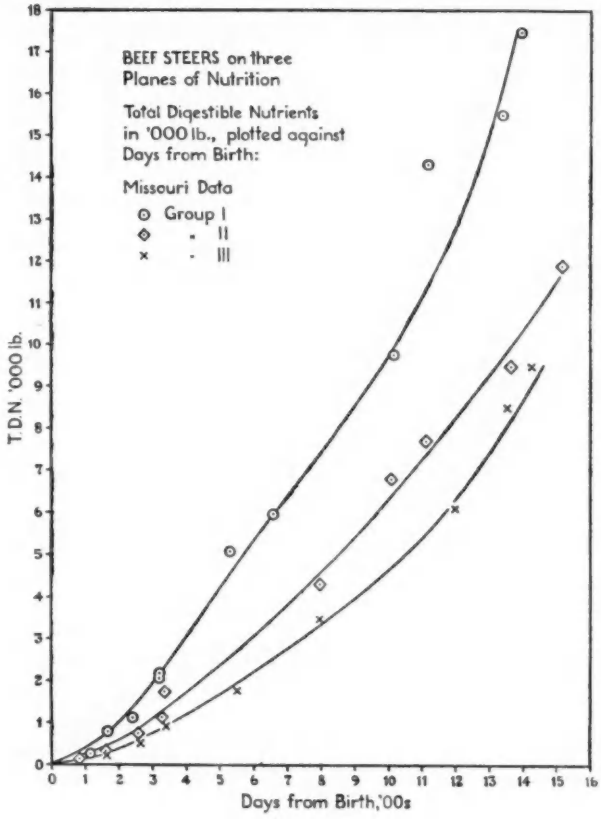

FIG. 13.

Many balance-sheets, some of which have been published (e.g. that by Norman Wright [8]), of the foodstuffs consumed by live-stock in Great Britain, and the production of and by animals have shown that the figures of starch equivalent given in Bulletin No. 48 of the Ministry of Agriculture and Fisheries, which have been used in these calculations, give an exceedingly accurate and reliable picture of conditions; they are in fact very well supported by realized results. Nevertheless, partly because we are working with American materials, I use 'total digestible nutrients' (T.D.N.) as a measure of food consumed.

Cumulative consumption of food by steers.—In Fig. 13 for each analysed animal of the Missouri experiment the T.D.N. consumed throughout life are plotted against the age at death in days from birth. The curves

drawn freehand through the points for each group are concave upward so that as the animal becomes older its food consumption per day increases, in fact, disproportionately to its weight. Two features of these curves should be noted: The curve for Group I is sensibly

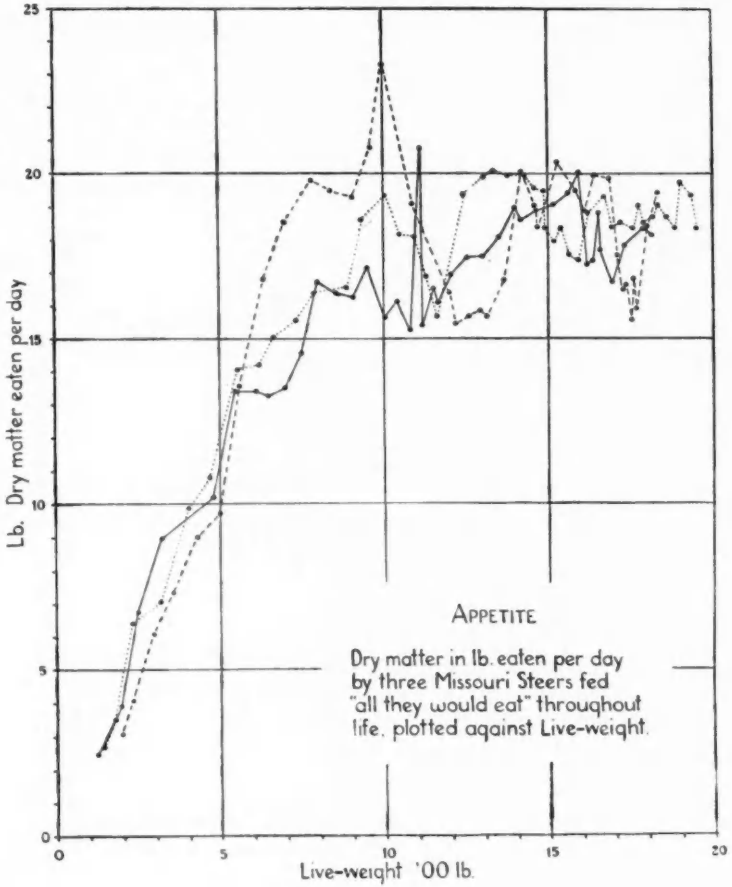

FIG. 14.

straight between 300 and 1,000 days, implying a constant rate of food consumption over this period, when very active growth is taking place; the curve for the Group III turns sharply upward after 1,200 days, implying an increased daily intake, which is associated with a definite storage of fat.

Appetite.—The fact that the curve of food consumption for the steers of Group I is evidently not that of any simple equation is explained by Fig. 14, in which the daily intake of food averaged over successive

periods of 30 days, and expressed as lb. of dry matter, is plotted against live-weight for three individual steers, which were fed 'all they would eat'. It is obvious that the curve representing appetite so measured is bipartite. From 100 to 1,000 lb. live-weight it steadily increases almost in proportion to the live-weight, but from this point onward the appetite remains sensibly constant. This phenomenon, which is also shown in a graph representing steers fed at Beltsville and at the Illinois Agricultural station [9], no doubt reflects the slowing down of growth at about 1,000 lb. live-weight and its effective end at about 1,400 lb.

It must, however, be remembered that the Missouri steers throughout life were fed on a ration which taken as a whole was unusually concentrated, and that it is therefore probable that the volume of their gut at any size was smaller than it would have been had they received a more bulky diet. Woodman [10] states that a steer weighing 1,800 lb. will eat 32½ lb. of dry matter p.d., more than 1½ times as much as the Missouri steers did in fact consume.

Efficiency of production of human food.—The efficiency of conversion of the animals' food into human food, if both be measured as lb. of Organic Product or in calories, is expressed by dividing the total life consumption of food by a steer by the amount of human food produced. In Fig. 15 this figure is plotted against live-weight at the time of slaughter. It is very obvious that the points for each group are related to an independent curve, the three curves diverging widely as they extend from a point of zero weight and an efficiency which is presumably about 1. Comparison of these curves with those for food consumption in Fig. 13 shows that the difference between them must depend on the differing rates of feeding, and that doubling the level of nutrition increases the efficiency of conversion at 700 lb. live-weight from 2·7 per cent. to 13·0 per cent., that is, to 4·8 times. It must be understood that this is a partial efficiency only; the full treatment will be found in Section V.

Further, it is remarkable that whereas the efficiency of Groups II and III falls off very rapidly with increasing weight, that for the very much heavier cattle of Group I shows only a very slight decline, from 16 per cent. at 700 lb. to 11·8 per cent. at 1,200 lb. and 10·5 per cent. at 1,900 lb. These facts are in no way unexpected, because maintenance of an animal for one day without any increase in weight involves the oxidation of a definite amount of food, and only food eaten in excess of this amount can be used for growth or fattening. The daily intake of food by the steers of Group III was so little in excess of their requirements for maintenance that little growth and less fattening occurred. But the unexpected way in which the curve for Group I tends to become parallel to the horizontal axis depends on the fact that the increase in weight from 1,200 lb. onward is almost entirely fat and a little water, and that not only has fat a very high calorific value, but as the proportion of fat in the body rises so does the proportion of the total energy content of the body that is edible increase.

The facts are extremely striking: they show beyond dispute the importance of feeding beef cattle at the highest possible level of food-intake if they are to produce human food in the least uneconomical way.

Effect of a store period.—The Minnesota experiment, if we may judge by the published figures, gave for those full-fed steers that are comparable in rate of food-intake with Group I of the Missouri series an efficiency of some 14 per cent. for animals weighing from 1,000 to

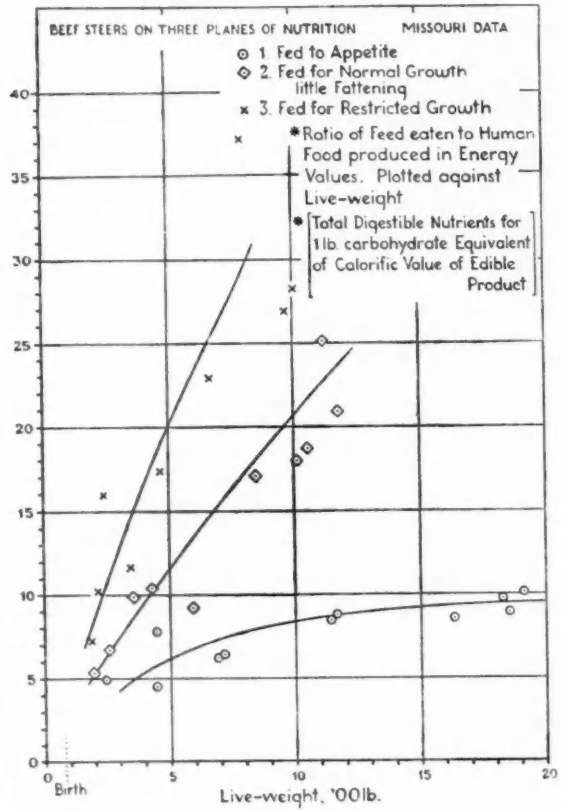

FIG. 15.

1,400 lb. Some steers in this experiment spent a summer grazing and were then full fed until slaughter. Of these seven were analysed so that their yield of human food can be determined.

So far as can be estimated from the recorded food consumption, these steers after their return to full stall-feeding showed an efficiency of production of human food measured in calories which did not differ significantly from that of cattle full fed throughout their whole life, over the same range in weight. This evidence, which though scanty is all that exists, thus suggests that, although it is notorious that store cattle may make spectacular live-weight gains when they are put on to heavy

feeding, the efficiency of production of human food which they attain is no greater than that of steers of similar weight full fed throughout life. That in fact this period of rapid fattening does not do anything to make up the loss involved in the extension of the period of life and hence of maintenance which is the effect of a store period [11].

Efficiency of production of edible protein.—The diet of the Missouri steers consisted of milk, hay, and a standard corn mixture; thus the crude protein contained in it when reduced by digestibility coefficients is an adequate measure of actual protein intake because the uncertainty introduced by the presence of 'amides' is absent.

Thus the total amount of protein digested during life after birth, divided by the amount of edible protein yielded after slaughter, is an adequate measure of the cost of producing this human food.

The points for individual animals are plotted against live-weight in Fig. 16, which shows that, as was to be expected, the efficiency of conversion by the rapidly growing animals of Group I was greater than for Group II, which itself was more economical than Group III. But as the amount of protein needed for maintenance is small compared with that used for growth, the divergence of the three curves is very much less than it is for edible energy produced (cf. Fig. 15). Further, the efficiency of conversion falls off very rapidly as the animal increases in size, the rate of fall being steeper for the steers less well fed.

Thus the most economical stage at which to kill a beef animal, if protein be the all-important constituent, is a bobby calf. But, even for the production of protein it never pays to starve an animal or even to feed it to a level lower than that which its appetite allows it to eat.

It is a realization of this fact, probably unconsciously acquired as a result of practical experience, which has led continental Europe to eat veal to an extent much greater than in England. Indeed beef, other than that produced by cows cast from dairy herds, is fed only in wealthy countries like England and the U.S.A. or under ranching conditions in South America and Australia.

Physiological cost of growth and fattening.—Since any reduction of elaborate processes to simpler terms capable of mathematical expression is valuable in that it enables prediction to be made of the results of modes of treatment which have not been experimentally investigated, it is important to try to split up the food-intake of the Missouri steers into parts devoted to maintenance and production, and hence to determine the actual physiological cost of the processes of growth and fattening which lead to the conditions found in an animal when slaughtered. In such an investigation we are concerned with the total amounts of protein and fat in the body, wherever they be situated.

Maintenance cost.—The total amount of digestible nutrients which had been eaten by the Missouri steers by any day is represented graphically in Fig. 13. The next stage is to determine the amount required for maintenance. This quantity has been well investigated, perhaps better for dairy heifers than for beef steers, but the results are in good agreement. All the available evidence has been discussed by Brody [12], who concludes that the maintenance-requirement varies as the 0·73

power of the live-weight, and expresses the result in a table of the amount of T.D.N. needed for maintenance at any weight. The figures given by Woodman [10], which have proved by use to be reliable, represent a straight-line version of this curve, calculated on starch equivalent, but do not go below 500 lb. live-weight, because of the probable

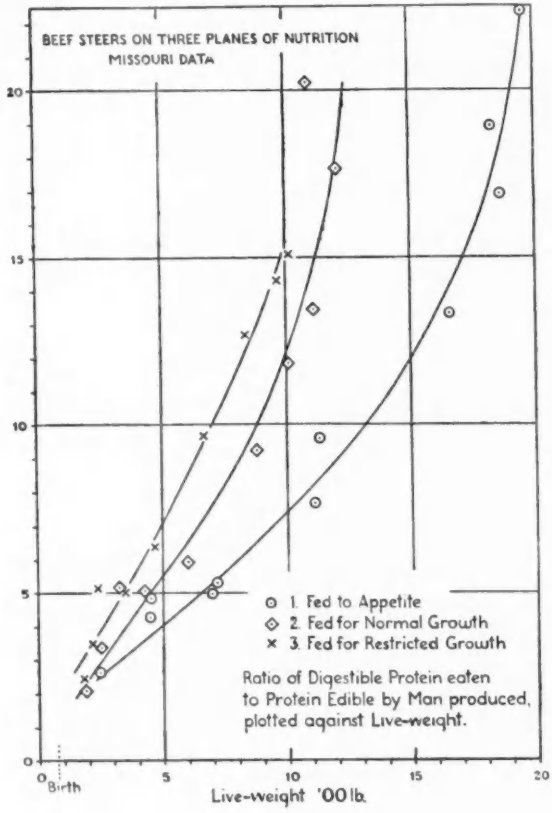

FIG. 16.

inaccuracies of the formula. We have used Brody's figures, which are in fact confirmed by those cases amongst the Missouri experiment in which individuals were held at constant weight. Owing to the irregular growth of individuals it is necessary to calculate maintenance in 30-day periods.

The accumulative maintenance required by the Missouri cattle is shown graphically by the points, which are generalized, freehand, in the broken lines, in Fig. 17. Owing to their higher weights at every age the curve for the Group I steers is always above that for Group II, itself regularly above that for Group III.

In Fig. 17 I have introduced from Fig. 13 the curves representing the total food-intake of the three groups. The distance between the broken line and the continuous line shows for each group the cumulative amount of food used for growth and fattening. It will be seen that the amount so available is very small in Group III when compared with

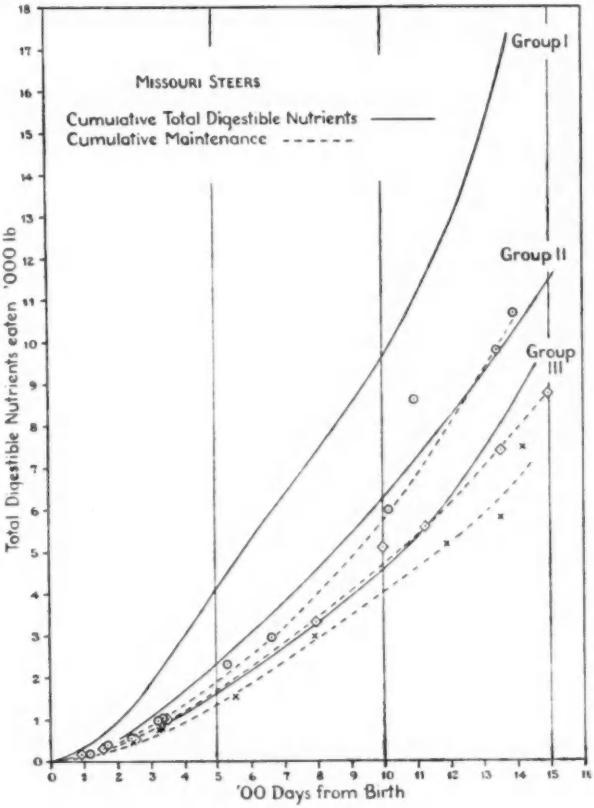

Fig. 17.

Group I, and the low efficiency of poorly fed animals is thereby explained.

Production cost.—But a further investigation of the conditions is most easily made by dividing the amount of Organic Product (energy) in the body at slaughter into T.D.N. it has had at its disposal for production. In Fig. 18 the figures so obtained are plotted against live-weight. It is at once obvious that below a weight of 400 lb. these figures are quite unreliable, indeed two of them are less than 1, which is impossible. The errors here are no doubt due to an overestimate of the amount needed for maintenance; the amount of Organic Product stored is very

small, and errors which would be negligible in larger animals have a very great effect. Nevertheless, it is evident that the efficiency of these animals is very high, above 50 per cent. With a single exception, a Group III steer at 950 lb., which is completely abnormal, all the points group well, though the scatter is considerable, as was to be expected. The freehand curve drawn through these points must express the general

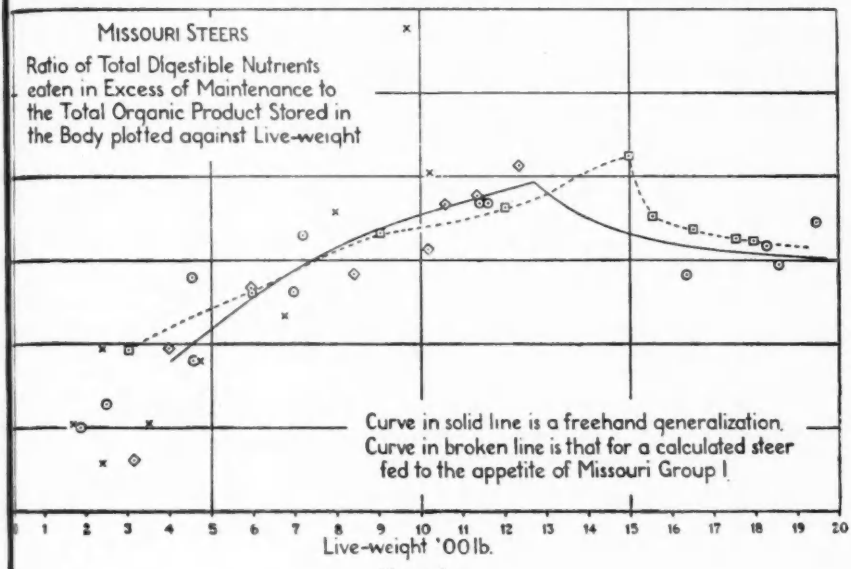
MISSOURI STEERS
Ratio of Total Digestible Nutrients eaten in Excess of Maintenance to the Total Organic Product Stored in the Body plotted against Live-weight
Curve in solid line is a freehand generalization.
Curve in broken line is that for a calculated steer fed to the appetite of Missouri Group I
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Live-weight '00 lb.

FIG. 18.

effect of changes in weight at any rate in its main character. It is to be noted that there is no tendency for any clustering of the individuals of the three groups about separate curves; clearly the physiological cost does not alter with the level of feeding.

In essence the physiological cost of storing materials, measured in energy values, in the body rises from 0 to about 1,250 lb. live-weight, and then decreases, the curve being to all appearance discontinuous. The character of this curve would be completely explained were the cost of protein storage, which is effectively the cost of making the fat-free body, to rise steadily as the animal approaches its maximum size, whilst the cost of storing fat with its very high calorific value remained constant, at a level less than that for protein at high weights. It is possible to investigate the validity of these two assumptions.

Protein for maintenance.—The total amount of digestible protein eaten by the Missouri steers is known.

Some protein is needed for maintenance, hair is constantly growing, skin is exfoliating and is constantly replaced, mucus is constantly lost from the alimentary tract, and other processes, probably in muscle, involve the breakdown of protein. This last, destroyed, protein is

largely excreted in the urine, and if an animal be fed on a nitrogen-free diet of adequate energy value, the daily loss of nitrogen in the urine may be held to represent the amount of protein broken down which must be replaced. The amount of digestible protein which must be eaten to replace it must in general be greater than what it produces in the body, because the amino acid make-up of most plant proteins differs

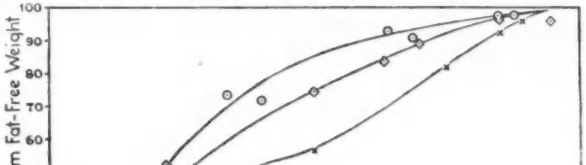

FIG. 19.

from those of animals' bodies. It is thus usual to multiply the protein equivalent of the urinary nitrogen on a nitrogen-free diet by a factor. The lowest which has been suggested for cattle is 2·0, by Mitchell [13]. I have used this figure because it seems to agree better than any higher one for the small cattle in Fig. 18.

It has been suggested that the amount of protein needed for maintenance varies as does the requirement of energy for maintenance. In fact, the maintenance requirement for protein is so small compared with that needed for growth that even doubling the figures I have used makes an inappreciable difference to the final result.

Growth-curves.—It is convenient in considering protein to express the amount in an animal's body as a percentage of that which can be accumulated when the animal reaches its maximum size. In fact, the marked uniformity of the contribution which protein makes to the total weight of the living parts of the body makes this figure almost the same as the fat-free live-weight similarly expressed. In Fig. 19 I have plotted the live-weight less fat of the Missouri steers as such a percentage against age in days from birth.

In accordance with expectation the three groups fall on well separated curves. That for Group I is the normal curve of growth for a mammal. Group II departs little from this curve, but Group III is markedly different, being irregular and over a long range approaching a straight line. These differences must depend on a limitation set by feeding-stuffs available for production. As the individuals of Groups I and II show a storage of fat at all ages to an amount clearly exceeding the 'Element Constant', it is evident that the limitation of growth of Group II is due

to protein shortage. And indeed it seems certain that the much delayed growth of Group III was similarly induced and did not depend on failure of calories for production.

If now we determine the amount of protein needed for maintenance by each steer in accordance with Mitchell's figures, and subtract this amount from the total amount of digestible protein eaten, we obtain the protein available for production, that is growth.

Cost of storing protein.—This figure for production protein, divided by the amount of protein in the whole body less a conventional allowance for that in the calf at birth, gives a ratio which is the amount of protein eaten in excess of maintenance to lay down one pound of protein in the body up to the time of slaughter.

If these ratios be plotted against live-weight less fat expressed as a percentage of the maximum which could be reached, we obtain the curve in Fig. 20, the points on which can be generalized by the freehand curve drawn through them. One important feature clearly shown is that the individuals of the three groups are related to a single curve.

It seems clear that between 20 per cent. and 75 per cent. this curve is nearly a straight line, and trial has shown that it cannot be represented by any exponential function.

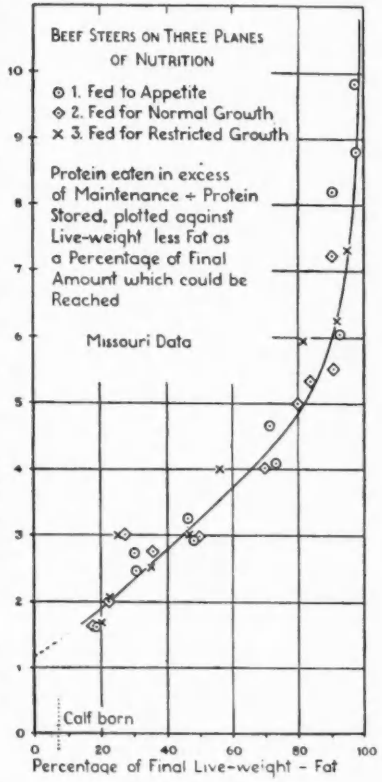

FIG. 20.

This curve can usefully be presented in another form. The interval vertically between its intersection with the lines at 10 per cent. and at 20 per cent. measures, when multiplied by 10, the amount of protein consumed to raise the amount stored by 10 per cent. of the final amount. By continuing this process we can determine the amount so needed at any weight. These points are plotted in Fig. 21. Here again it is clear that from 5 to 65 per cent. the curve is effectively a straight line, and that it suddenly rises to a very high level indeed as it approaches or exceeds 90 per cent. It has been held, and is perhaps generally believed, that this curve should follow the law of diminishing returns, but it does not in fact approach the curve representing that function; rather it is to be regarded as the straight line which it closely follows between birth and 65 per cent. There is no reason to expect a sudden discontinuity of the curve at this point,

and it is simplest to suppose that the straight line would continue to 100 per cent. The area included between this line and the actual curve would then represent protein eaten in excess of that needed for growth, which could be applied to other purposes, the supply of energy for

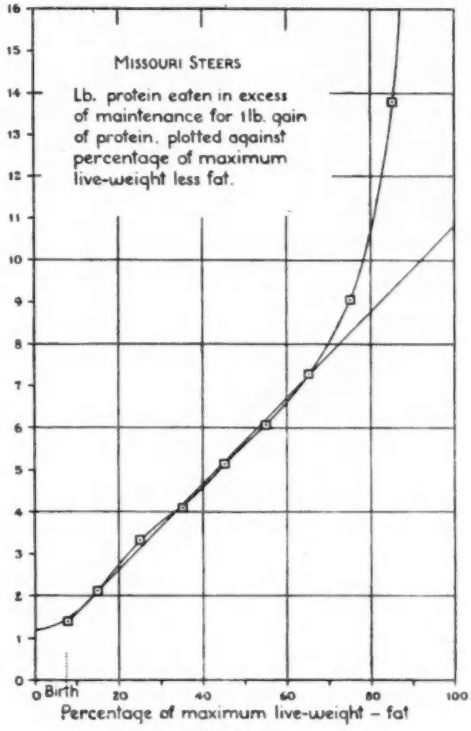

FIG. 21.

maintenance or for the storage of fat. It is perhaps significant that the three individuals of Group III which lie in this part of the graph are the only ones in that group which laid down an appreciable amount of fat.[1]

An excess of protein in the later stages of the life of these steers may readily have occurred. The food fed was uniform in chemical composition throughout, and it was eaten in great quantity by the large animals when actual growth was exceedingly slow (Fig. 19). Thus, if adequate, as it was, to allow of very rapid growth round 50 per cent., it is likely to have been in excess when 90 per cent. or more of the maximum size was reached.

Thus the first postulate made for the interpretation of Fig. 18, that the cost of laying down protein increased with size to a large amount, is justified.

[1] What happens to the energy contained in the protein needed to store 1 lb. of protein in excess of that which provides the aminoacids needed is unknown.

The practical application of this fact—that the ratio of protein to carbohydrate in the rations of large cattle should be less than in that for small beasts—has long been recognized.

Cost of fat-storage.—If we subtract from the total amount of food consumed by an animal the cumulative amounts used for maintenance and that which has been consumed in growth, essentially the addition of protein, we are left with a residue which can be used for the storage of fat.

All the errors of the calculations are accumulated in this final figure. These errors arise in many ways; the determination of the amount used e.g. for maintenance depends on a formula extrapolated for a long way in both directions beyond the region in which it has been experimentally investigated. The cost of protein-storage involves a maintenance cost whose magnitude is subject to the same causes of error as general maintenance, and the equation which we have used for determining its amount is itself of an unexpected character, and may misrepresent the facts. Animals may have individual idiosyncrasies, their digestion or assimilation may be abnormal, they may possess a physiology or a diseased condition which hinders fat deposition, or causes them to waste energy by movements greater than those normal to the herd. All these errors will be related to the live-weight, and only to the extent to which this live-weight depends on fat to the storage of that substance. And all these errors are ultimately conveyed into the estimate of the food available for fat-formation, an amount which in the extreme case where 40 per cent. of the whole body is fat does not exceed one half of that used for other purposes. Round 17 per cent. fat it is of the order of one-sixth, at lower fat percentages it becomes very small. Thus the proportional effect of these errors is magnified more for the small and thin than for the large and fat animals, and the scatter of the points representing individual animals can be expected to be great, decreasing for the heavier steers.

If we express this amount of food available for fattening in the form of cost per pound of fat laid down and plot this value against live-weight, we obtain Fig. 22.

It is evident that the scatter of the points on the graph, which includes only steers of 500 lb. live-weight or more, though considerable, is less than might reasonably have been expected. It has the expected character of being greatest at low weights and least for heavy fat animals.

Certain points, the two Group I steers at about 1,100 lb. and the four Group I steers at the right, are probably more reliable than the others. It seems therefore justifiable to hold that it shows that there is no steady increase in the cost of storing fat with increasing live-weight and fatness.

Therefore, like the first, the second postulate we made in explaining the peculiarities of the curve expressing the physiological cost in terms of energy of growth and fattening related to live-weight (Fig. 18) seems to be justified.

If we generalize the points in Fig. 22 by the freehand curve drawn through them, we can, by determining the rate of protein storage from Fig. 19 and the food available for production from the data of

Fig. 17, calculate the physiological cost of growth and fattening of generalized individuals of Groups I and II. The curve in broken line in Fig. 18 passes through such calculated points. It will be observed that it fits the actual experimental points very well, and that its most remarkable character is the sudden drop at about 1,500 lb. live-weight. The original freehand curve through the points is thus in essence justified.

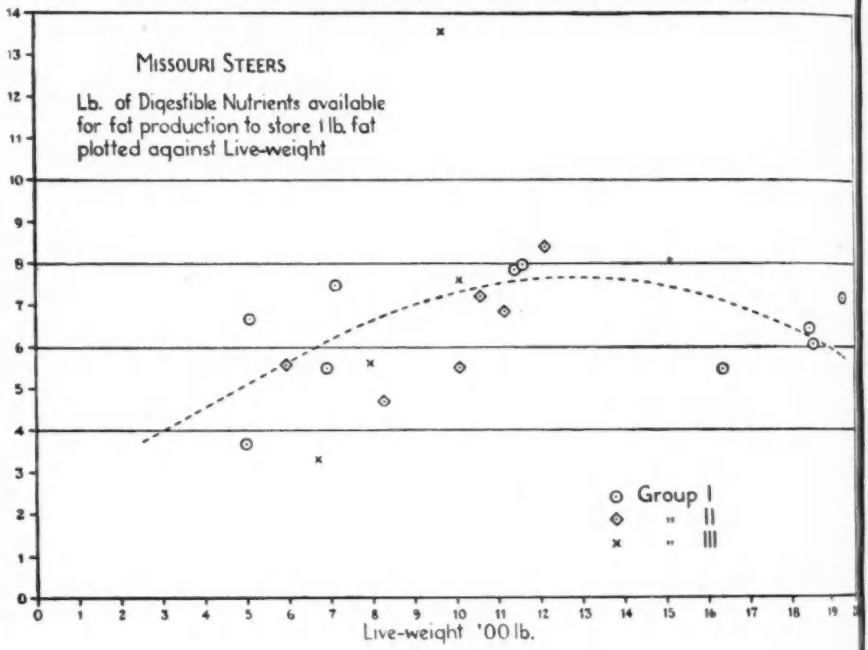
Missouri Steers
Lb. of Digestible Nutrients available for fat production to store 1 lb. fat plotted against Live-weight
Group I
" II
" III
Live-weight '00 lb.

Fig. 22.

The character of the empirical curve in Fig. 22 for the efficiency of storage of fat is unexpected. I can see no reason why the cost should increase from 500 lb. to 1,200 lb. live-weight and then decrease again. The actual form may depend on an incorrect determination of the maintenance requirement of small and of large cattle.

I have used Brody's figures because they have been adopted by a conference of the U.S.A. National Research Council. But these figures do not agree with those calculated by Gullickson and Eckles [14] for the maintenance of dairy cattle, being higher at weights below 200 lb., much lower in the range 400–1,000 lb., and again greater above 1,400 lb.

I have recalculated maintenance requirements using Gullickson and Eckles figures, and find evidence that in the range 400–1,000 lb. they must be considerably too high, but think it reasonable to believe that the low requirement of the formula for heavy weights is correct. I am also prepared to believe that the maintenance requirements calculated from Brody's formula are too large for small animals.

If these conclusions be justified, then it is not improbable that the curve in Fig. 22 should really be a straight line at a constant level of about 7·0 lb. of T.D.N. used for the storage of 1·0 lb. of fat in a beef steer at any weight or fatness. This represents an efficiency on a calorific basis of about 32 per cent.

The total efficiency of milk production has repeatedly been calculated and is of the order of 60 per cent. of the available digestible energy. The efficiency of the secretion of protein and lactose in milk is not known, but may well be of the same order as that of the conversion of milk protein into body protein by the sucking calf, which may be around 70–75 per cent. If it be so, then the efficiency of fat-secretion into milk will be of the order of 45 per cent., higher but not very greatly so than the figure reached above for the storage of fat in the body.

I have presented the foregoing series of calculations of the physiological efficiency of the storage of protein and fat in the body of beef cattle with considerable hesitation because of the obvious errors which may exist in them, but the whole subject is one of such difficulty and importance that I felt it desirable that some analysis of the admirable data of the Missouri experiment should be made purely empirically by a zoologist who would not be unduly influenced by such minor factors as the effect on total digestibility of different mixtures of food. In any case the mode of extraction of the figures expressed in the graphs of this paper is such that they can be used in calculating the character of the steer which will be produced by feeding at a definite level both for T.D.N. and for protein at various stages of growth and fattening. As it is evidently impossible to express the rate of growth by an equation, the calculation must be done for each short period and is laborious.

V. *The Optimum Point at which to Slaughter Cattle*

The practical end to which this paper has been directed is the determination of the most economical point at which to slaughter beef cattle, and this fortunately does not involve any elaborate calculation liable to large errors.

If we plot the weight of edible Organic Product contained in the carcass and offals against the Total Digestible Nutrients eaten from birth to slaughter, we obtain three curves, one for each group, Group I, fed to appetite, consuming more than twice its maintenance requirement until its members weighed 1,200 lb. and then dropping to a consumption over its whole life of 1·6 times maintenance. Group II ate about 1·4 times maintenance throughout, and Group III a little less than 1·2 times maintenance throughout.

These curves (Fig. 23) are remarkable because above about 600 lb. live-weight the gain of edible calories is nearly proportional to the food consumption, the curves becoming near to a straight line and showing only a very slowly decreasing return as the steers become larger.

The enormously greater return for a given amount of food yielded by the well fed steers is vividly shown. But it is also evident that the yield per 1 lb. of food consumed becomes progressively less as the animal grows bigger, i.e. if the process of beef production be assumed to start with the new-born

calf, then it becomes more and more uneconomical as time goes on. But in fact it does not then begin, and further analysis is necessary.

We import steers and heifers from Eire for feeding. These animals come to us when about 2 years old weighing some 700 lb.; they are fed for a period of about 6 months and are then slaughtered at a weight of 1,100–1,200 lb., i.e. if full fed they fall on to the curve of Group I in

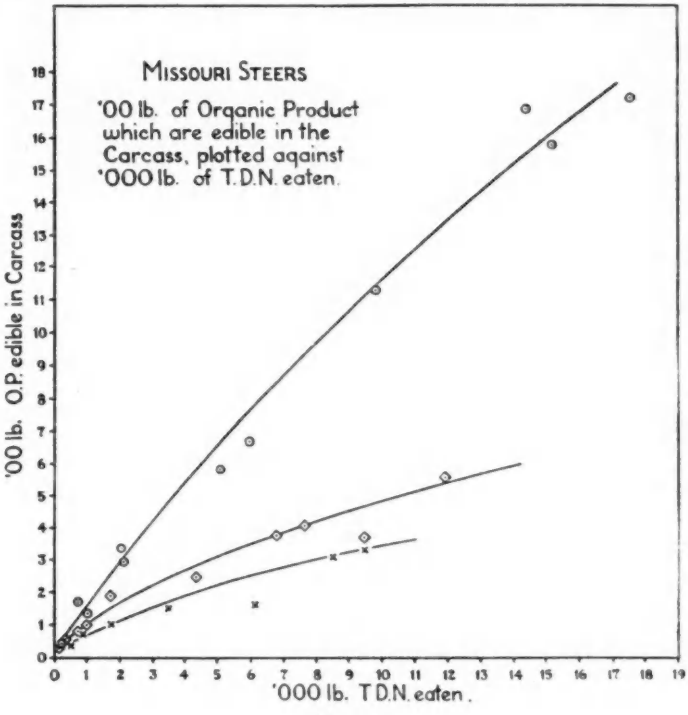
MISSOURI STEERS
'00 lb. of Organic Product which are edible in the Carcass, plotted against '000 lb. of T.D.N. eaten.
'00 lb. O.P. edible in Carcass
'000 lb. T.D.N. eaten.

FIG. 23.

Fig. 23, between 2,000 and 6,000 lb. food-consumption. If they were fed only at the rate of Group II they would fall between 3,000 and 12,000 lb. food-consumption and would have eaten twice as much food for the same amount of increase in human food. But the larger part of the steers and heifers fed for beef in Great Britain were bred in this country. To an unknown but certainly large extent these were produced by dual-purpose cows whose primary function is the provision of milk for human consumption, but a proportion, larger in Scotland than in England, were borne by cows of beef breeds which produce a negligible amount of milk and serve only to bear calves intended to be reared and fattened for beef. These latter animals must therefore carry the cost of the maintenance of their mothers for the year which includes their life from conception to birth and the period of lactation during

which they consumed all or nearly all the milk yielded by the cow, about 220 gallons.

But in addition they might be charged with a proportion of the cost of rearing their mother to the time when she produces her first calf. This proportion is determined by the total number of calves she produces during her whole life, a figure unknown for beef cows, but of the order of 4 for dairy cows. But as the cow herself is ultimately slaughtered for beef it is perhaps fair to regard the cost of her production as met by the yield of human food she gives at death.

It is easy by a simple graphical construction to determine the most economical point at which to slaughter cattle if these factors be taken into consideration.

All that is necessary is to continue the horizontal axis of Fig. 22 to the left beyond zero, and carry along it the cost of maintenance and milk-production of the cow for 1 year, starting from the calorific value of the milk she has yielded. A tangent to the curve of production by the steer drawn from the point which represents the year's cost of the cow will then touch the curve at the point of maximum efficiency because the tangent will represent yield as a definite proportion of the food consumed, i.e. it will express a definite constant efficiency throughout the intra-uterine and extra-uterine life of the steer, and both below and above this optimum weight the curve of production will fall below this proportionate yield (Fig. 24).

For Group I, full-fed, the optimum is at a live-weight of about 1,740 lb., with a fat percentage of 35 and an actual killing-out percentage of 64.

For Group II the optimum is at a live-weight of 1,100 lb., with a fat percentage of 15 and an actual killing-out percentage of about 59.

For Group III the figures are live-weight 800 lb., fat percentage 9, actual killing-out percentage 58.

These figures for the weight and character of steers giving the highest return in human food for feeding-stuffs consumed apply only to beasts fed at a regular level throughout their lives.

They cannot be directly applied to the majority of British beef cattle. The steers of the Missouri experiment were fed 'uniformly' throughout their life, i.e. the daily intake of T.D.N. was a definite proportion of the maintenance requirement on any one day for each steer of each group.

But the steers fed for beef in Great Britain have a different history. As calves they may or may not be fully fed, but the majority of them at some time pass through a store period during which their daily food-intake is little greater than their maintenance requirement, so that they make only small live-weight gains and store little fat. They are then fed on a high level, making large live-weight gains and storing much fat.

It is evident that the whole curve representing the relation of human food produced by cattle so fed to their consumption of T.D.N. will lie between the curves for Groups I and III in Fig. 23, being roughly parallel to that of Group III for the store period and to that of Group I for the fattening period.

The effect is to raise the weight at which maximum total efficiency is reached, and to lower the efficiency of the whole process.

The effect of charging a proportion of the cost of producing the cow to the beef cattle is to raise the optimum weight, fatness, and killing-out percentage.

The optimum weight at which to kill beef cattle if they are valued solely on their yield of protein edible by man can be similarly determined, the cost being expressed in amount of protein digested.

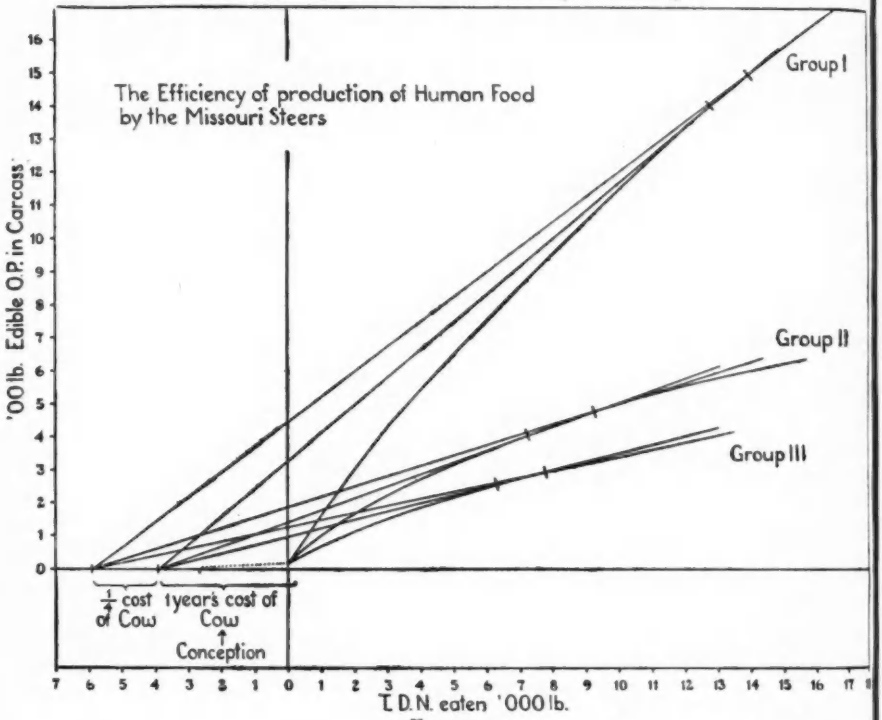
The Efficiency of production of Human Food by the Missouri Steers
Group I
Group II
Group III
'00 lb. Edible O.P. in Carcass
T.D.N. eaten '000 lb.
¼ cost of Cow
1 year's cost of Cow
Conception

FIG. 24.

For Group I: about 840 lb. live-weight, fat 22 per cent., actual killing-out percentage 60.

For Group II: 640 lb., 14 per cent. and 54 per cent. are about the optimal figures.

For Group III: 450 lb., is the optimum weight.

In times of peace, in a wealthy country, protein and palatability will be of greater proportionate value than total calorific yield, and even during war palatability so far from being negligible is perhaps of very great importance; 'hunger is the best sauce', but men employed for long hours in sedentary occupation may need the encouragements of flavour to induce them to eat a sufficient bulk of carbohydrates and to set up an adequate flow of digestive juices.

It is therefore useful to try to discover some rational basis for valuing the various constituents of beef. Two possible procedures are evident:

(1) It is generally held that in a temperate climate a normal man should eat 25 per cent. of his total calorific intake in the form of fat and that about 12 per cent. of his total food should be protein. Good quality beef contains about 25 per cent. of fat and 15 per cent. of protein, the calorific value of the fat in a given joint being about 3·7 times that of the protein. If we decide that the palatability is of such importance that the fat and the protein contained in such beef are of equal value, that is that beef may be valued on the dry matter it contains, then the optimal points of slaughter are for Group I at 1,700 lb. live-weight and for Group II at 1,008 lb.

(2) The only direct quantitative measure of the value which the ordinary man places on protein and palatability is the price he is prepared to pay for it. Milk contains protein, fat, and sugar and is a constituent which adds to the palatability of many prepared foods. A gallon of milk sells for 28*d*.[1] and at the price of margarine and cane sugar the price of the fat and lactose contained in it is 4½*d*. Thus the protein it contains plus the palatability, vitamins, and minerals is valued at 23½*d*., roughly 72*d*. per pound of protein.

Beef, bone-free, costs about 15*d*. per pound, of this 25 per cent. is fat valued at 2*d*., so that the 15 per cent. of protein it contains plus the palatability is valued at 13*d*. This is 86*d*. per lb. of protein. Thus common taste as expressed in the price it is prepared to pay values the protein and palatability of animal products at about 9 times as much as fat.

Thus if we express the value of the product of a beef steer at its protein-content plus one-ninth of its fat-content we may be expressing common taste. On this assumption the peace-time optimum at which to kill beef steers of Group I is 1,150 lb. live-weight, fat percentage 24, and actual killing-out percentage 59.

These figures are remarkably close to the actual average figures of cattle which before the present war earned a quality subsidy. But it is obvious that in war-time, when all fats are rationed and in short supply, the relative value of the fat in beef will increase, and the optimum weight at which to slaughter cattle will more nearly approach the 1,740 lb. which is the appropriate figure for full-fed cattle valued on an edible energy basis.

But the fattening of imported steers presents a special problem. These animals are of good beef-quality and must have come from cows whose main function is the rearing of calves and not the production of milk. The price paid for them must therefore include the maintenance of the cow. And the price is in effect paid by exportation from this country of goods which represent a definite amount of labour, power, and materials which could in principle have been devoted to growing the food necessary for their production in this country. Thus the optimum point to slaughter these imported cattle could be determined by plotting back from the point at which they enter an equivalent in cattle-food of the money expended in their purchase, i.e. the optimum cannot differ greatly from that of home-bred cattle fed at the same rate.

Cattle which are a by-product of the dairy herd may be viewed in the

[1] These are war retail prices and are lowered by subsidies. But they serve to illustrate the general level of appreciation.

same way; the money paid for the calf represents an amount of feeding-stuffs expended in feeding the cow which produced them, in excess of that she requires for milk production. But this amount is so small that the optimum weight at slaughter will be very low, in fact the Continental custom of basing agricultural organization on the production of milk and veal is thoroughly justified.

We are now in a position to make a real estimate of the efficiency with which beef cattle convert their own food measured as Total Digestible Nutrients into human food measured in terms of Organic Product, i.e. of energy.

If charged with one year's maintenance and production of the cow, the maximum efficiencies are: Group I 8·6 per cent., Group II 3·7 per cent., Group III 2·6 per cent.

The maximum efficiency of conversion of digestible protein in feeding-stuffs into protein edible by man is for Group I 10·5, Group II 8·7, and Group III 7·6 per cent. The efficiency thus varies much less with changes in feeding than the efficiency of conversion of energy.

The maximum efficiency of conversion of T.D.N. eaten to edible dry matter is extraordinarily low: Group I 4·3, Group II 2·0, Group III 1·4 per cent.

Summary and Conclusions

THE foregoing paper contains an analysis of the data of a Missouri University experiment in which a large number of beef steers were fed from birth on one or other of three different planes of nutrition, individuals in each group being slaughtered and analysed at successive stages.

It is shown that the calorific value of the human food yielded by a steer is a constant proportion of the live-weight for any given percentage of fat in the whole body, and that the edible protein in the body is proportionate to the live-weight with small variations dependent largely on the fat-content.

As the growth and fattening of the body proceed at the expense of the food eaten in excess of that used for maintenance (a function of live-weight), it follows that the efficiency of production of human food, either protein or calorific value, rises steeply with a raised level of nutrition to a limit set by appetite and the possible concentration of digestible materials in the diet.

The efficiency of production of human food falls with increasing weight, the fall in calorific value being relatively small for beasts fed at the highest practicable level, but very steep as the daily food-intake is reduced.

The maximum size, measured by the fat-free body-weight or the amount of protein in the body, which can be attained is greater for full-fed stores than for those reared at any lower level of nutrition. The cost in terms of protein digested in excess of that needed for maintenance to store 1 lb. in the body increases arithmetically by the same amount as the animal increases by a constant percentage of the maximum size which could be reached at any level of nutrition.

The cost of storing fat shows no steady increase with size or increasing fatness. It may, indeed, be constant.

It follows that any period (a store period) in the life of a steer in which it is fed at less than the maximum possible rate inevitably reduces the efficiency of the production of human food. The cost of producing a fat ox which has been born to a cow of beef breed, which does not yield any milk for human consumption, must include the cost of maintaining the cow for one year.

Under these conditions the optimum point of slaughter can be found graphically, and the efficiency of the whole process determined.

For steers fed at what must be nearly the highest possible level (that which produces baby beef) the optimum, if beef be valued on its calorific value, is at 1,740 lb. live-weight, fat percentage 35, and actual killing-out percentage 64.

If beef and the feed used in making it be valued only on protein, the optimum is 840 lb. live-weight, fat 22 per cent., actual killing-out percentage 60. And if beef be valued, as common taste seems to show it is, by its protein-content + its fat-content divided by 9, the optimum is 1,150 lb. live-weight, fat percentage 24, and actual killing-out percentage 59, a figure very near to that of cattle which earned a quality subsidy before the war.

But the highest efficiency achievable in the production of beef is, if the product be valued in calories, only 8·6 per cent.; or for protein 10·5 per cent.

The optimum point of slaughter for steers born to cows in milk herds, in which the cost of maintenance of the cow is chargeable to the milk sold, is at birth.

Or if the very small additional cost of the foetus be charged to the calf, and not to the milk, then the optimum point of slaughter may be at about two months old, when the calf yields good veal.

Thus the highest efficiency however measured is attained by steers fed, as are baby beefs, on the most concentrated possible foods at the highest possible level.

And a store period so reduces the efficiency that it is only justifiable as a mode of salvaging grazing and feeds for which no other use can be found.

APPENDIX

The equations and graphs contained in this paper allow us to determine, with large probable error, the course of development of a beef steer when fed on any given diet at a defined level. The process is as follows:

Suppose we feed a steer weighing 800 lb., containing 140 lb. of protein and 65 lb. of fat on a diet of which 20 lb. of dry matter yield 12·6 lb. T.D.N. containing 0·875 lb. digestible protein. Fig. 14 shows that the steer can eat 20 lb. per diem.

Brody's figure shows that the maintenance requirement of such a beast is 5·73 lb. T.D.N. per diem.

Mitchell's figure for protein needed for maintenance is 0·294 lb. p. d.; or, 0·875 lb. of protein is actually eaten so that each day 0·875 − 0·294 = 0·581 lb. can be used for growth.

The steer contains 140 lb. of protein and when growth ceases may be expected to have 177; it is therefore 79 per cent. of full size. Fig. 21

shows that it must use 8·8 lb. of available food protein to produce 1 lb. of protein in the body; it therefore adds 0·066 lb. p. d.

In 30 days this is 1·98 lb. of protein stored. Fig. 4 shows that this will be about 17·5 per cent. of the live-weight less fat added, i.e. the live-weight less fat increases by 11·3 lb. Fig. 19 shows that such a rate of growth is possible.

The remaining food may be used for fat production. It is in lb. of T.D.N., 12·6 eaten p. d.−5·73 lb. for maintenance−0·58 lb. protein used for growth = 6·29 lb. T.D.N. available for fat production. Fig. 22 shows that at 800 lb. live-weight about 6·3 lb. T.D.N. are needed to produce and store 1 lb. of fat. Thus 1·0 lb. of fat is stored per diem.

During 30 days 30 lb. of fat and 11·3 lb. live-weight less fat are added to the body and the steer at the end of the period weighs 841 lb. and contains 142 lb. of protein and 95 lb. of fat, 11·3 per cent. Fig. 7 shows that such an animal yields from its carcass 190 lb. of edible Organic Product. The process can be continued indefinitely. After 180 days the steer should weigh 1,019 lb. containing 151 lb. protein and 243 lb. of fat, having made a live-weight gain of 219 lb. in 180 days.

The points connected by the broken-line curve in Fig. 18 were calculated in this way. The accuracy with which they fit actual experimental points is some justification of the method.

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THE FEEDING-VALUE OF FLAX BY-PRODUCTS

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THE feeding-value of flax by-products attracted little attention in this country so long as the home-grown crop was almost entirely dam-retted. Flax straw is not normally de-seeded prior to dam-retting; during retting a proportion of the bolls drop off and are lost, and the chaff of those which remain after retting, drying, and stooking has lost much of its fermentable carbohydrate. The by-product of the subsequent scutching is usually a mixture of broken stem and woody shive along with the remaining bolls, and is of comparatively little use as a feeding-stuff. It is frequently utilized as boiler fuel in scutch-mills.

The introduction of green scutching on an extended scale since the outbreak of war and the necessity for saving home-grown seed have altered this position. Before green scutching the bolls are removed by combing and then processed for seed-recovery. The chaff usually retains a small proportion of seed, but consists essentially of broken empty seed-capsules and their pedicels. The seed is processed to remove dirt and dust; the flax seed is then separated and the residue of broken and light seeds is utilized as feeding-linseed; it is variable in quality and may contain weed seeds (e.g. *Ranunculus* and *Polygonum* spp.).

Since flax is also de-seeded before tank-retting, the probable extension of this process is likely to contribute to the proportion of flax by-products which will become available for feeding purposes.

Linseed and feeding-linseed.—The feeding-value of linseed is well known and is referred to here merely for comparison with by-product 'feeding linseed'. Good Northern Irish samples of linseed usually contain about 35 per cent. oil, but the oil-content of feeding linseed tends to be lower and in the neighbourhood of 23 to 28 per cent. (Table 1). This is due to (*a*) presence of weed seeds of lower oil-content than linseed, and (*b*) the relatively large proportion of lighter and immature seeds of relatively low oil-content. The fibre-content of feeding-linseed tends to be higher than that of pure linseed.

Samples of commercial feeding-linseed were found to contain from 79 to 99 per cent. linseed by weight, up to 9 per cent. weed seeds by weight, and in one case as much as 12 per cent. of small crumbs of earth. In spite of the purity of one sample containing 99 per cent. linseed, its oil-content was only 26·8 per cent.; it consisted mainly of light seeds.

Whole flax bolls.—Whole flax bolls are not likely to be available for feeding so long as it is necessary to save the maximum proportion of seed. However, under normal conditions it might prove convenient to dispose of some of the flax by-products as ground, entire flax bolls, and analyses are given in Table 1. From what is known of the feeding-value of linseed and of flax chaff, it can be estimated that the starch equivalent of ground, entire flax bolls will be about 85.

Flax chaff.—The average linseed-content of the whole bolls (including

TABLE 1. *Composition of By-products of Northern Irish Flax*
(Figures in brackets indicate minima and maxima)

	Moisture	*Crude protein*	*Ether extract*	*N-free extract*	*Crude fibre*	*Ash*
	%	%	%	%	%	%
Linseed (seed-quality)	11·0	22·7	34·4	22·1	5·8	4·0
'Feeding linseed' (5 samples)	10·0 (8·9–11·1)	23·5 (20·1–25·2)	26·0 (23·9–28·3)	26·3 (24·4–27·2)	9·6 (7·0–12·4)	4·6 (4·1–9·6)
Ground, whole bolls	14·0	20·0	24·3	25·9	17·0	5·1
Flax chaff, freed from seed	12·1	7·0	2·4	33·5	38·3	6·7
Commercial flax chaff (7 samples)	12·7 (10·4–15·5)	8·0 (6·1–9·6)	5·0 (2·2–8·4)	35·1 (29·1–41·8)	32·2 (29·7–36·0)	7·0 (6·3–7·6)
Shive (dam-retted flax)	9·9	2·6	1·1	24·4	57·5	4·5
Shive (green scutching)	9·2	8·7	7·6	25·2	42·5	6·4

TABLE 2. *Composition and Feeding-value of Northern Irish Flax Chaff*

		Moisture	*Crude protein*	*True protein*	*Oil*	*Soluble carbo-hydrates*	*Crude fibre*	*Ash*	*Starch equivalent*[2]
Average Northern Irish flax chaff (sample 1); unretted[1]	Total	13·55	9·03	8·24	5·42	32·33	32·70	6·97	29·1
	Digestible	—	5·42	4·63	3·98	10·20	14·88	—	
Average Northern Irish flax chaff (sample 2); unretted[1]	Total	15·38	9·63	8·72	6·38	29·13	32·19	7·29	26·5
	Digestible	—	6·26	5·35	4·51	7·63	12·69	—	
Flax chaff (Kellner)	Total	11·6	3·5	3·1	3·4	35·0	40·7	5·8	17·7
	Digestible	—	1·4	1·0	1·7	13·0	12·2	—	
Meadow hay, good (*Rations for Livestock*)	Total	14·3	9·7	8·1	2·5	41·0	26·3	6·2	31·3
	Digestible	—	5·4	3·8	1·0	25·7	15·0	—	
Meadow hay, poor (*Rations for Livestock*)	Total	14·3	7·5	6·0	1·5	38·2	33·5	5·0	19·1
	Digestible	—	3·4	2·5	0·5	19·3	15·6	—	

[1] Average result of two digestibility trials.

[2] Starch equivalents calculated from digestibility data as described in text.

pedicels) of 5 fibre varieties was 66·4 per cent.; complete separation of seed from clean bolls should, therefore, yield about 2 cwt. chaff for every 4 cwt. seed. In practice, however, about 3 to 4 cwt. chaff are secured for every 4 cwt. seed, for the chaff frequently includes more or less broken stem, dried leaf, weed fragments, &c., as well as the broken capsules, whilst a small proportion of lighter seed is usually left in the chaff. This proportion is variable, but 10 per cent. is frequently present in samples which may seem at first sight to contain very little seed. It has been found that attempts to secure a more complete recovery of seed may defeat their object by leading to mechanical injury of the seed.

Analyses of flax chaff are given in Table 1. The oil-content of samples from which all residual seed had been carefully removed was between 2 and 3 per cent. Samples whose oil-content is much above this value will contain more or less residual seed, and commercial Northern Irish flax chaff usually has an oil-content of 5 to 6 per cent., although some samples are lower.

The only data accessible to the writer for the digestibility of flax chaff were those given by Kellner in *The Scientific Feeding of Farm Animals*, but the analysis of his sample suggests that it did not contain any seed, and it may have been more fibrous than the chaff of modern fibre varieties as grown in Northern Ireland. Accordingly, digestibility experiments were carried out with sheep using two typical samples of commercial Northern Irish flax chaff, which contained about 11 per cent. by weight of residual flax seed. Two experiments were conducted using two sheep as subjects in each experiment, and the results are set out in Table 2. The experiments were conducted in the usual manner with collection of faeces over a 10-day period. The flax chaff proved very palatable to the sheep, and 2 lb. per day was readily eaten by sheep of 90 to 100 lb. live-weight. All the starch equivalents in Table 2 have been calculated from the digestible nutrients by Kellner's method, using the factor 2·3 for oil (which flatters the 'oil' of hay, but is probably nearly correct for the oil of commercial flax chaff), and correcting for fibre by subtracting crude fibre $\times 0{\cdot}58$ from the gross S.E. values in the case of the hays (long fodder) and crude fibre $\times 0{\cdot}29$ in the case of the flax chaff. The calculated values for S.E. have not been adjusted by increasing the calculated Kellner S.E. by 20 per cent., as is the case with the values for hays in *Rations for Livestock*.

It is clear from Table 2 that this flax chaff had a feeding-value rather less than that of 'good meadow hay', but better than that of 'poor meadow hay' or oat straw. The digestibility of the nitrogen-free extract was curiously low, especially as the digestibility of the fibre was of the same order as that of hay. However, this is compensated by the superior content of digestible oil in the flax chaff.

These particular samples of flax chaff contained about 11 per cent. by weight of flax seed, mainly light seeds encased in capsule fragments. If a S.E. of 100 be assigned to this residual linseed, then somewhere about one-third of the total S.E. of the chaff was due to its residual linseed. Clearly any increase in extraction of seed during de-seeding will render the chaff closer to poor meadow hay or oat straw in feeding-

value, and determination of the oil-content or a direct separation of the seed present will give an indication of the feeding-value of the sample. The sample examined by Kellner was distinctly inferior in feeding-value to the usual type of flax chaff now offered for feeding in Northern Ireland.

It may be pointed out that the data given in Table 1 enable one to form approximate estimates of the proportions of chaff and seed in ground mixtures of flax seed and flax chaff.

The fibre of flax chaff.—A few analyses were made in order to compare the 'fibre' fraction of flax chaff with that of cereal straws and oat hulls. The data are set out in Table 3. Although both the crude fibre of the flax chaff and its content of fibre, as determined by Norman's method, are less than in oat straw, it will be noted that its content of lignin is more than twice as great and is comparable with that of oat hulls. The analyses tend to confirm the view that flax chaff completely freed from linseed will have a feeding-value little better than that of oat straw or poor meadow hay.

TABLE 3. *Analyses of Cereal Straws and Oat Hulls Compared with Flax Chaff* (all figures on dry matter basis)

	Wheat Straw	*Barley Straw*	*Oat Straw*	*Oat Hulls*	*Flax Chaff (commercial)*
Crude protein .	2·1	2·9	2·2	1·5	10·4
Ether extract .	1·4	2·0	1·6	2·6	6·3
N-free extract .	46·2	45·0	46·7	52·5	37·4
Crude fibre . .	43·9	42·5	41·9	39·9	37·8
Ash . . .	6·4	7·6	7·6	3·5	8·1
Lignin[1] . .	9·9	8·2	7·2	13·6	15·3
Fibre by Norman's method[2] . .	53·3	52·5	53·5	47·0	45·7
'Cellulose'[3] . .	43·5	44·2	46·3	33·4	29·3

[1] Lignin was determined by the sulphuric-acid method and the crude lignin corrected for ash and protein contents.

[2] Norman's method comprises extraction of the fat-free material with 5 per cent. W/V H_2SO_4. The weight of the dried residue is corrected for ash and protein content and the resulting figure gives an estimate of 'cellulose + lignin' [1].

[3] 'Cellulose' = Fibre by Norman's method − lignin.

Other residues from threshing and scutching operations.—Debris from sieving and the dust from winnowers are practically worthless for feeding, and may contain large amounts of acid-insoluble ash. Broken flax stems and waste flax or tow are quite useless and are usually refused by stock.

Shive from dam-retted flax is practically useless, and at best is inferior to oat hulls in feeding-value. Shive from green scutched flax may have a better analysis than ordinary shive owing to presence of some bolls and seed, the shive from various mills varying in this respect, but it is in practice worthless as a feeding-stuff. Flax chaff containing appreciable amounts of shive should be avoided.

Summary

1. 'Feeding-linseed', being the residue from the dressing of home-produced flax seed, has a feeding-value about five-sixths of that of pure linseed owing to presence of more or less weed seeds and of a large proportion of lighter immature seeds.

2. Commercial flax chaff has a feeding-value slightly inferior to that of good meadow hay, but superior to that of poor meadow hay or oat straw. The feeding-value of completely de-seeded flax chaff might be little better than that of oat straw or poor meadow hay.

3. Other residues from processing of flax, e.g. broken stems, waste tow, dust from winnowers, shive, &c., have no practical feeding-value.

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CORRIGENDA

Vol. X, No. 40, p. 221, par. 3, last 2 lines, *read* '. . . since the treatments were stopped at the end of 1935'.

Vol. XI, No. 42, p. 80, line 11, *read* '. . . the most effective one. Although, more theoretically . . .'

—— p. 81, line 36, *read* 'The crop loss over the mealy-bug area during this period is not thought to have been less than 5 per cent.'

—— p. 82, line 13, *read* '. . . many useful indigenous herbs, and shrubs . . .'

—— p. 85, column headed '1938' line 17, for '375' *read* '275'.

—— p. 100, lines 16 and 22, and Plate 1, legend, for (above) *read* (a), for (below) *read* (b).

—— p. 110, line 13, add as footnote: Unpublished note 1935–6: Larger form Termes (Cyclotermes) sp.; smaller form Microtermes thorocalis Sjöst. 'Mortality amongst young cotton plants was invariably caused by the latter, whereas the (wooden) pegs were attacked by both.'

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